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# REPRODUCTIVE AND PHYSIOLOGICAL CYCLES IN AN ISLAND POPULATION OF NORWAY RATS<sup>1</sup>

B Y

RICHARD M. LATTANZIO<sup>2,3</sup> AND JOSEPH A. CHAPMAN<sup>2</sup>

## INTRODUCTION

The importance of the Norway rat (*Rattus norvegicus* Berkenhout) in the study of animal populations as well as its detrimental effects on man's economy and health necessitates the understanding of the factors which regulate populations of this species. Due to the close association of the Norway rat with human populations, investigations of this rodent have been largely limited to those populations influenced by human activity. This direct or indirect dependency on man for various degrees of food and harborage may in turn affect the reproductive and physiological parameters of the Norway rat. Consequently, past studies of Norway rats may not accurately represent these parameters under wild conditions. Comparative data is lacking on Norway rat populations void of human influence. The present study was initiated in order to examine the effects of population density and climatic variations on an isolated, independent island population of Norway rats. The interrelationships of reproductive and physiological parameters with population density and climatic changes were examined and compared to previously published data.

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St. Clements Island in southern Maryland supports a unique population of wild Norway rats. Emigration and immigration are limited due to the distance between shorelines (0.68 km). The island is uninhabited by man and there are few predators. The small size of St. Clements Island also offers the advantages of a corresponding reduction in the diversity of flora and fauna as well as reduced variation in climatic changes as compared to the mainland (MacArthur and Wilson 1967). In addition, the influence of the surrounding water produces a buffering effect, moderating short term temperature extremes (Moyer 1978:2). In general, St. Clements Island constitutes a comparatively simple, natural unit of study, void of many factors which could mask the effects of environmental and climatic changes.

Resident mammalian species present on the island also include the eastern cottontail (*Sylvilagus floridanus*) and the muskrat (*Ondatra zibethicus*). Due to differences in the habitat and food requirements of these species, neither would be expected to have any major competitive effect on the Norway rat population (Martin et al. 1951; Godin 1977).

Observations during the study period revealed evidence of mink (*Mustela vison*), great horned owl (*Bubo virginianus*) and a northern harrier (*Circus cyaneus*). These potential predators or their sign were observed on only one occasion each. It was assumed that their effects on the rat population was negligible.

In the absence of significant immigration, emigration and predation, the effects of density and climatic variation on population regulation can be more fully assessed. A thorough understanding of Norway rats in a natural environment can be of importance in the control of rat populations.

The Norway rat is the most extensively studied species in the order Rodentia. Its status as an ideal experimental subject and its notoriety for causing economic damage and epidemical problems has led to voluminous literature on the biology of the albino and domestic strains. Albinism and domestication, however, are factors which modify behavior

(Huck and Price 1976; Price and Huck 1976), physiology (Mosier 1957), morphometrics and reproduction (H. H. Donaldson 1924:339; Castle 1947). Consequently, the albino and domestic strains cannot be compared legitimately to the wild genotype.

Past investigations of Norway rats have been directed predominately toward urban populations (Perry 1945; Davis and Hall 1948; Davis and Hall 1950; Davis 1951a, b, c, d; Davis 1953; Brown et al. 1955; Christian and Davis 1956). These populations are characterized by their high degree of dependence on high density human populations for food and harborage. Studies of rural Norway rats (those populations which live in association with low density human populations and are dependent on man to a lesser extent) have been conducted under captive situations (Calhoun 1963; Andrews et al. 1972) and natural conditions (Errington 1934; Davis 1948, 1949a, 1951a). Significant differences have been shown to exist between urban and rural rats in Baltimore, Maryland (Davis 1949a, b; 1951a). These include differences in growth rates, maximum weight, weight at sexual maturity and various reproductive parameters. As these differences can be related to the degree of man's influence on environmental conditions, it is hypothesized that the St. Clements island population will exhibit characteristics similar to rural rats, as compared to urban populations.

Reproductive data from investigators worldwide led Davis (1951d) to conclude that Norway rats exhibit a surprisingly uniform natality. Reproductive parameters such as ovulation rates, litter size, pregnancy and lactation rates tend to range around a similar mean for any particular area or time period. However, a degree of variation can be expected due to local environmental conditions and specific population differences. These conditions will have an effect on the productivity of a specific population. It has also been shown that certain long-term stress factors exert a significant influence on reproductive parameters, irrespective of environmental and climatic fluctuations (Christian 1963b).

The effects of long-term stress was first described by Selye (1936) as the General Adaptation Syndrome (GAS). According to this concept, a species undergoes three stages of

adaptation to continued stress. During this adaptation period, stress elicits certain hormonal responses of the hypothalamus-hypophysis-adreno-cortical axis and results in physiological changes in body organs. Numerous investigators have demonstrated, invitro and insitu, that prolonged stress is counteracted by physical changes in the endocrine organs. Changes in the adrenal glands, thyroid, pancreatic islets, posterior pituitary and spleen have been related to a number of physiological and morphological changes in response to stressful stimuli (Christian 1963b; Selye 1973). These changes have been found to play an important role in the regulation of animal populations.

Studies of the role of physiological feedback mechanisms on controlling population levels have been primarily focused on the adrenal glands. Selye (1939) observed that, in addition to eliciting adrenal response, various stress stimuli also inhibited reproduction. Christian and Lemunyan (1958) observed that mice crowded invitro resulted in suppressed growth of progeny for two generation, lowered pregnancy rates, implantations and number of young weaned. Male mice responded similarly to artificial high densities by a decrease in the weight of reproductive organs and an increase in adrenal weight (Christian 1959). Christian (1963b), in his summary of endocrine adaptive mechanisms, reported a positive relationship between adrenal hypertrophy and population density which results in a decrease in reproductive activity in both males and females.

Various types of stress stimuli have been associated with adrenocortical hypertrophy in the Norway rat. Among them are high population densities (Christian and Davis 1956), social rank (Barnett 1955) and climatic changes (Andrews et al. 1972). These factors, individually or in combination, can produce depression of a population's productivity.

Similarly, changes in splenic weight has been utilized as an indicator of stress in mammals (Christian 1963b). Splenic hypertrophy has been found to occur in pregnant mice (*Peromyscus leucopus* and *Mus musculus*) (Davis et al. 1961) and in albino mice under artificial high density conditions (Christian 1959). Decreases in splenic weights have been observed in a high density population of cottontails (*S.*

*floridanus*) under severe weather conditions (Conaway and Wight 1962:288). Willner et al. (1979) also reported decreases in splenic weights of nutria (*Myocastor coypus*) which corresponded with severe winter weather.

#### ACKNOWLEDGEMENTS

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#### STUDY AREA

Research was conducted on St. Clements Island, located on the Potomac River approximately 32 k northwest of the Chesapeake Bay in Saint Mary's County, Maryland (Fig. 1). The island has been eroded from 162 ha in 1634 to the present 18.2 ha. Distance from shorelines is 0.68 km.

The general soil composition of St. Clements Island is a Matapeake-Mattapex-Sassafras association. This soil type is characterized by moderate to well drained soils of silt-loam and a sandy substratum (Gibson 1978:9).

The island has four separate vegetation zones (Fig. 2). The northern end (Area I) is 3.8 ha of sandy loam soils with a pH of 5.6. Area I is primarily beach and tidal marsh habitat containing scattered stands of Virginia pine (*Pines virginiana*) and black locust (*Robinia pseudoacacia*). Understory species include eastern red cedar (*Juniperus virginiana*),

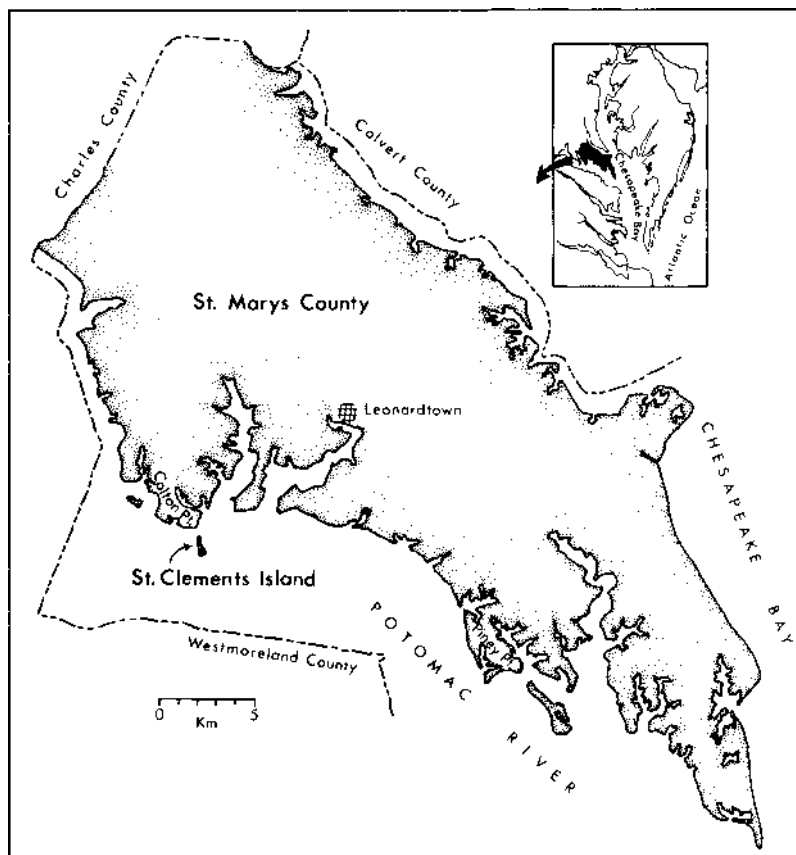


Fig. 1. Location of St. Clements Island, Potomac River, St. Marys County, Maryland.

scrub oak (*Quercus ilicifolia*), southern red oak (*Quercus falcata*), paper mulberry (*Broussonetia papyrifera*), black mulberry (*Morus rubra*), mimosa (*Albizia julibrissin*), great mullein (*Verbascum thapsus*), shining sumac (*Rhus copallina*), pokeberry (*Phytolacca americana*), wax-myrtle (*Myrica cerifera*), blackberry (*Rubus* sp.), swamp rose (*Rosa palustris*), thistle (*Cirsium* sp.), goldenrod (*Solidago* sp.), flowering spurge (*Euphorbia corollata*), Virginia creeper



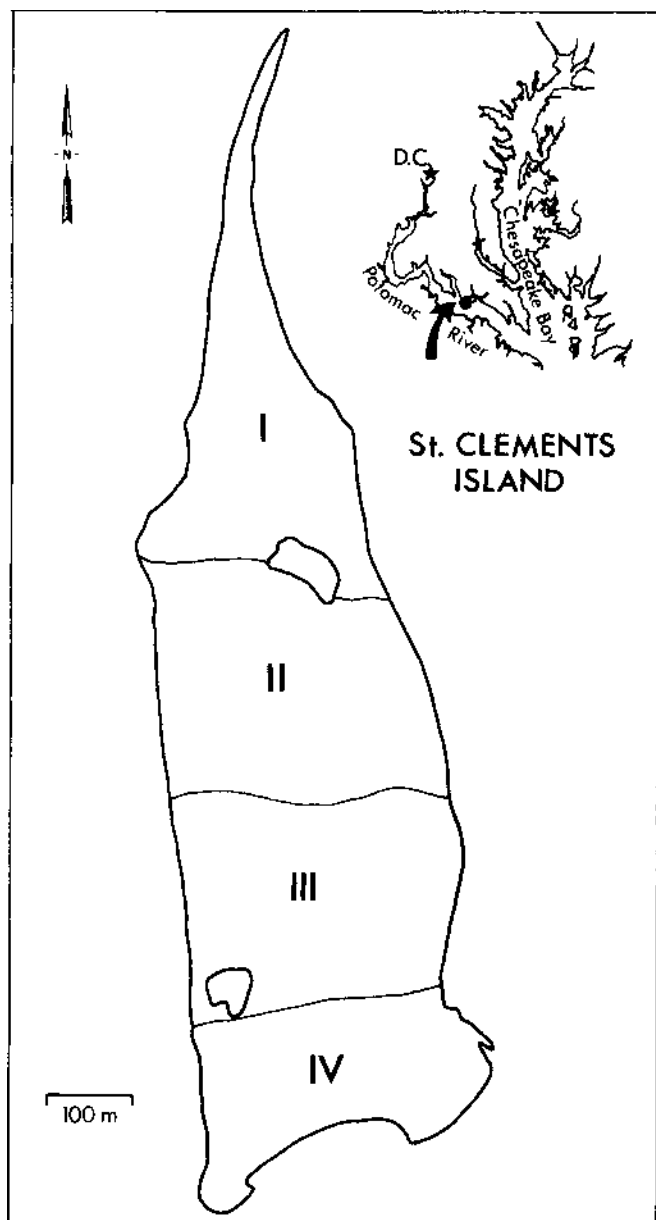


Fig. 2. Vegetation Zones on St. Clements Island.

(*Parthenocissus quinquefolia*), Japanese honeysuckle (*Lonicera japonica*) and prickly pear cactus (*Opuntia drummondii*).

Area II is separated from Area I by a 0.12 ha pond. Area II has a loamy soil of pH 7.4 and is two to three meters higher than Area I. This difference in elevation excludes Area II from the occasional floodings occurring in the lower areas. Approximately 6.2 ha, Area II is dominated by high tide bush (*Baccharis halimifolia*), with an interspersed of white sweetclover (*Melilotus alba*). Other species which occur on Area II include wood sage (*Teucrium* sp.), black walnut (*Juglans nigra*), white mulberry (*Morus alba*), trumpet creeper (*Campsis radicans*) and moth mullein (*Verbascum blattaria*), as well as pokeberry, swamp rose mallow, thistle, goldenrod, shining sumac, black locust, Japanese honeysuckle and wax myrtle.

Area III is approximately 5.3 ha of poorly drained loamy soils with a pH of 5.7. Area III as well as Area II is maintained as a management area by the Maryland Wildlife Administration. Strips of these two areas are mowed annually to increase habitat diversity. The dominant vegetation of Area III includes trumpet creeper and high tide bush. Additional species found in this area include crimson eyed rose mallow (*Hibiscus palustris*), smooth sumac (*Rhus glabra*), swamp rose mallow, flowering spurge and white sweetclover.

The southernmost portion of the island (Area IV) consists of approximately 2.8 ha of loamy soil with a pH of 7.1. The southeastern corner supports a stand of eastern cottonwoods (*Populus deltoides*) whereas the southwestern corner supports a dense growth of salt marsh fleabane (*Pluchea purpurascens*), climbing false buckwheat (*Polygonum scandens*), white mulberry, black walnut, pokeberry, goldenrod, shining sumac and white sweetclover. The midsection of Area IV is mowed annually as a recreation area and is composed of *Graminae* and *Cyperaceae*.

#### CLIMATIC CONDITIONS

St. Clements Island has four well defined seasons. Temperature extremes are influenced by the Potomac River and Chesapeake Bay. The coldest period of the year occurs in

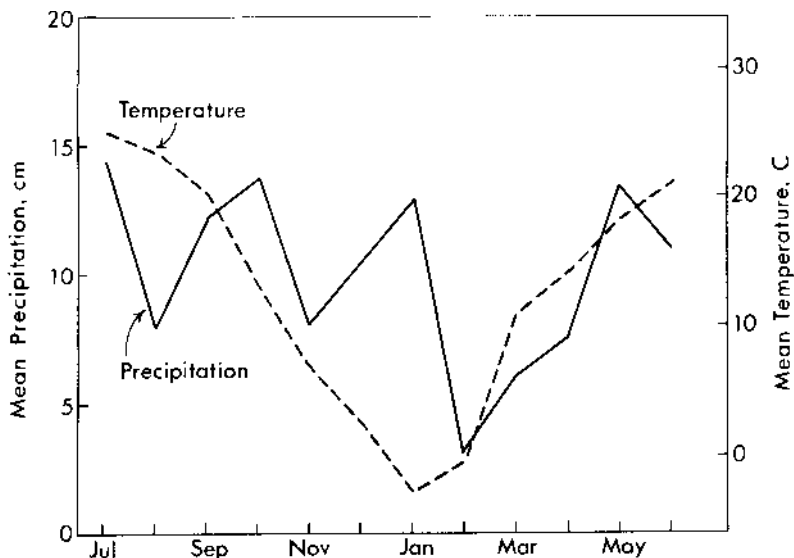


Fig. 3. Seasonal Mean Temperature and Precipitation on St. Clements Island (August 1976 - February 1978).

late January and early February with a yearly average of  $14.4^{\circ}\text{C}$ . Average annual precipitation is 104.3 cm. The months of June and July are generally the wettest while January or October is usually the driest (Figs. 3 and 4). Prevailing winds are from the west-northwest to northwest at 14.5 km per hour which becomes southerly in the warmer months. Freeze free days average 201 days per year and the growing season ranges between 180-200 days per year (Moyer 1978:2).

## MATERIALS AND METHODS

### FIELD COLLECTIONS

Norway rats were collected from August 1976 through February of 1978. Trapping was conducted for one 2 night period at monthly intervals. In addition, one 3 night and two, 2 night trapping periods were conducted in December 1976, October 1977 and November 1977 respectively, due to

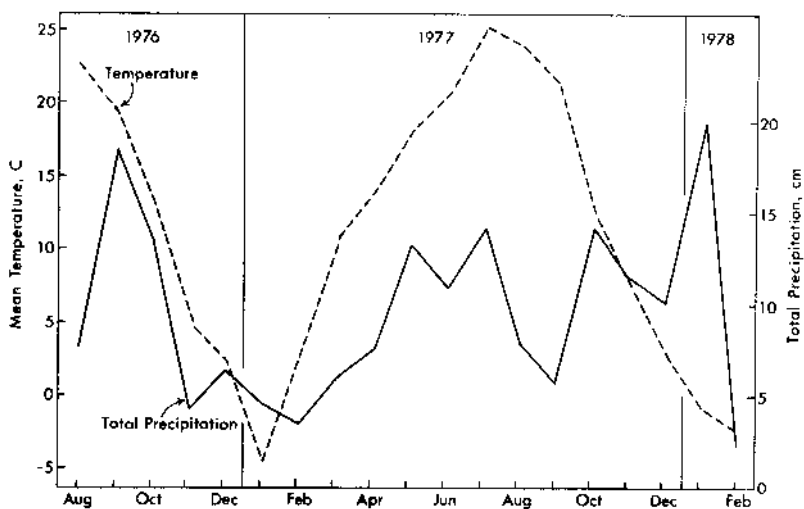


Fig. 4. Mean Temperature and Precipitation on St. Clements Island ( August 1976 - February 1978).

the lack of trapping success at normal intervals. Tomahawk live traps (15.2 x 15.2 x 45.7 cm, 6" x 6" x 18") were placed in suitable appearing habitat for the first night of each 2 night and the first two nights of the three night trapping periods. An average of 130 Victor Brand Four-way Release, Break-back rat traps were used on the last night of each trapping period. Snap traps were placed approximately 10 paces apart, along the perimeter of the island and baited with peanut butter. All traps were checked the morning after they were set.

Live-trapped rats were sexed by the presence or absence of mammary glands and testes protrusion (Wirtz 1972). Captured rats were tagged with size one, crimping pliers as close to the head as possible to prevent tag loss. Toe clipping was used as a positive reference in case of tag loss. No more than one toe per foot was clipped allowing a maximum of 98 animals to be marked (Giles 1971:307). Rats were then released at the site of capture.

Population estimates derived from live trapping data were based on a modified version of the Peterson Index. Discrete time intervals were not utilized due to the low sample size. However, combined trapping periods yielded estimates of population number which were believed to be representative of the actual number of rats present during that particular period. The index (Bailey 1952) was defined

$$\frac{(n+1) M}{(m+1)} \text{ as } N = \text{where:}$$

$N$  = the population estimate,

$n$  = the total number of rats collected in the sample period during the trapping period,

$M$  = the total number of rats marked and released during the trapping period,

$m$  = the number of recaptures

Variance of this estimate was calculated as described by Seber (1973) by the formula:

$$V = \frac{M^2 (n+1) (n-m)}{(m+1)^2 (m+2)}$$

Rats trapped for necropsy were immediately weighed to the nearest 0.1 gram on a triple beam balance. The eyeballs were removed and placed in a 10 percent buffered ( $\text{CaCO}_3$ ) formalin solution. Carcasses were stored in plastic bags and refrigerated until necropsies were performed.

#### POSTMORTEM EXAMINATIONS

Measurements of rat carcasses were: (1) total length (from tip of nose to tip of tail fully extended); (2) tail length; (3) foot length; (4) ear length from notch; and (5) K-value (length from tip of nose to tip of hind foot of the fully extended rat). Rats were then examined for ectoparasites and abnormalities.

#### NECROPSY PROCEDURES

Most rats were necropsied fresh, although some were stored frozen for later study. Reproductive organs, adrenal glands, heart, liver, spleen and kidneys were debrided of connective tissue and weighed to the nearest 0.001 of a gram

on a top loading Mettler Balance (Model P 163). The adrenal glands, spleen and reproductive organs were then preserved in Bouin's fluid.

#### Males

The reproductive organs of the male rats were dissected and examined. The cauda epididymides and testes were separated and individually weighed. Smears were made from the fluid of both organs and examined microscopically for the presence of mature sperm. Relative amount of sperm was recorded as absent, few, moderate or abundant, corresponding to a scale of 0 to 3. Male rats were considered reproductively active if moderate or abundant amounts of sperm were found in the epididymides. The testis and epididymides were then preserved in Bouin's fluid.

#### Females

The female reproductive systems were dissected and examined for visible signs of pregnancy, resorbing embryos and placental scars. Distance from the ovaries to vagina was measured and ovaries were stripped of the bursa and weighed to 0.001 of a gram after being fixed in Bouin's fluid for a minimum of twenty-four hours. Measurements of length, width and depth of the ovary was recorded and the ovary was then placed in an autotechnicon automatic tissue processor. This processor clears, infiltrates and dehydrates the tissues to be stained. Air pockets were then removed from the tissues by means of a vacuum pump and the tissues were embedded in paraffin and cooled. The tissue embedded paraffin block was then transferred to a rotary microtome where sections, ten micra thick, were cut. Ribbons of tissue resulting from the sectioning were placed in a heated water bath and affixed to a glass slide with albumin. The slides were then stained with hematoxylin, mounted and examined for corpora lutea.

#### SEX AND AGE

The sex of Norway rats was determined by internal examination of the reproductive organs. Fetal sex ratios were determined by internal examinations of well developed fetuses.

Adult, subadult and juvenile age classifications were determined by a combination of factors including eye lense

weight (Donaldson and King 1937; Friend 1967), body weight (Hirata and Nass 1974; Leslie et al. 1946) and reproductive condition (Perry 1945:25). Fetal age was estimated for rats by the condition of the uterine horn and approximate fetal weight (Emlen and Davis 1948:62).

Eye lens weight was obtained by removing the lens from the eyeball and drying the lens for 19 hours at 120 C. Weights were recorded within 2 mg on a FPE precision balance.

#### PRODUCTIVITY ESTIMATES

Average litter size was determined by counting the number of viable fetuses in the uteri of pregnant females and placental scar counts of nonpregnant females. Ovulation rates were estimated by examining the ovaries for the number of active corpora lutea. Females with active corpora lutea and no viable embryos were considered to have bred within seven days (Davis 1953:380). The difference between the mean litter size and ovulation rate was considered the intrauterine mortality rate. Resorption rates were determined by counting the number of resorbing embryos in pregnant females. The onset and duration of the breeding season was determined by the criteria used to denote pregnancy and embryonic age and then correlated to season.

#### CONDITION INDICES

Condition index (K), adrenal index (AI), spleen index (SI) and the body fat index (BFI) were used to compare the physiological state of rats, independent of size and weight (Chapman et al. 1977; Willner et al. 1979).

The condition index which relates to the general physical condition of the animal is defined as:  $K = \text{condition index} = W/L^3$ , where W is the weight in grams and L is the greatest length of the rat, described previously as the K value (Bailey 1968; Davis and Hall 1951). This formula gives a numerical reference which compares the weight of rats, assuming a uniform greatest length. Corrections for weight variations of pregnant females is not considered, since embryo weight is not significant until a few days prior to parturition (Davis and Hall 1951:13).

The weight of adrenal glands provides an acceptable index to adrenocortical activity due to physical or environmental

stress (J. C. Donaldson 1924; Christian and Davis 1956; Christian 1963a; Goertz 1965; Myers 1967). As an individual experiences long term stress, stimulation of the zona fasciculata by ACTH causes hypertrophy of these cells and results in an increase of adrenal mass which in turn increases the weight of the gland (Christian 1963b:246). Therefore, individuals subjected to long term stress exhibit relatively higher adrenal weights. To allow for the differences in body weights of individuals, the adrenal index was defined as the relationship of adrenal weight to body weight, where  $AI = \text{adrenal weight (mg)} / \text{body weight (g)} \times 10^{-3}$  (Chapman et al. 1977:18).

Changes in splenic weight has also been suggested as a possible indicator of stress for various species (Davis et al. 1961; Conaway and Wight 1962; Christian 1963b; Goertz 1965; Wirtz 1973). To determine the effects of stress on rats independent of size differences, the spleen index used in this study is defined as  $SI = \text{spleen weight} / \text{body weight} \times 10^{-3}$  (Willner et al. 1979).

The body fat index used was a qualitative estimate of fat reserves, converted to a four point scale. Rats were rated subjectively from one to four, the former indicating little to no fat deposits and the latter indicating very heavy fat deposits within the body cavity (Riney 1955).

#### STATISTICAL METHODS

A three way and two way analysis of variance with unequal subclasses and Duncan's New Multiple Range Test were used to analyze condition indices with respect to sex, age, and season. Binomial Probability Distributions and the students t-test were used where appropriate. Spearman's Rank Correlation tests were performed using the Statistical Package for Social Sciences (SPSS) (Nie et al. 1975). Correlation tests were utilized for each sex and age class as well as combined data and pregnant females. Statistical tests were considered significant when  $p < 0.05$  and highly significant when  $p < 0.01$ .

#### RESULTS

##### POPULATION ESTIMATION

One hundred-nine Norway rats were captured in 2083 trap nights, for a success rate of 5 percent. These animals were



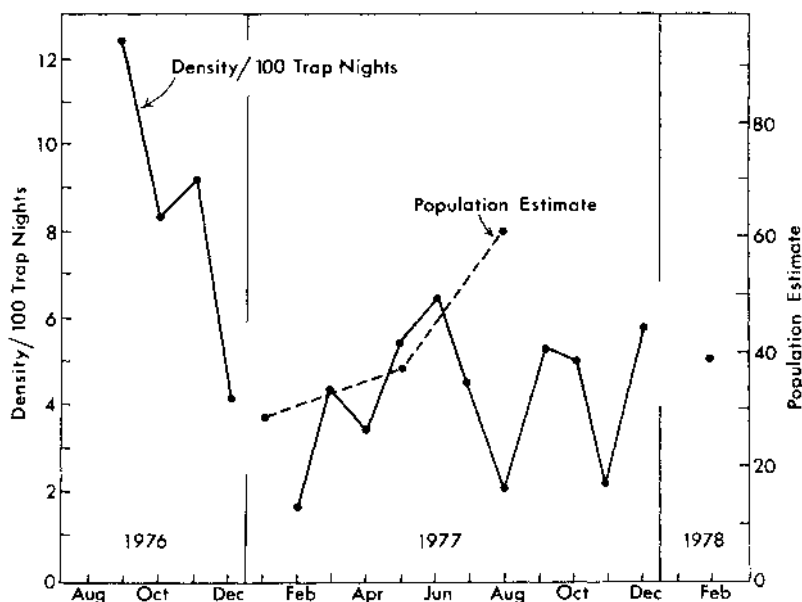


Fig. 5. Monthly Density Fluctuations of Norway Rats on St. Clements Island (1976-1978).

caught in snap traps and were used for necropsy. Relative abundance was determined by the number of rats captured per 100 trap nights for each month (Fig. 5).

Fourteen rats were taken in live traps, tagged and released. Eight of these rats were later recaptured. The mean population estimate for the sample period November 1976 to March 1977 was  $26 \pm 4$  rats. Estimated mean population size for the sample periods April to June 1977 and June to October 1977 was  $37 \pm 18$  rats and  $60 \pm 22$  rats, respectively (Table 1).

The maximum density of rats on St. Clements Island was determined to be 3.3 rats per hectare (1.5 rats per acre). Rats were estimated from trapping results, to occupy approximately 18 percent of the total island area.

#### AGE CLASSES

Three age groups were identified; juvenile, subadult and adult. Adults made up 55.7 percent of the sample, while

1980 TABLE 1. Lattanzio and Chapman, Norway Rats. TRAP NIGHTS, NUMBER COLLECTED, MARKED, RECAPTURED AND POPULATION ESTIMATES OF NORWAY RATS FROM ST. CLEMENTS ISLAND, 1976-78

Date	Trap Nights	Number Collected	Catch Per 100 Trap Nights	Number Tagged	Number Recaptured	Date Tagged	Population Estimate
8/76		3					
9/76	121	15	12.40				
10/76	121	10	8.26				
11/76	121	11	9.09	2			
12/76	125	5	4.00	2			
1/77							
2/77	120	2	1.67	1			
3/77	46	2	4.35		2	11/76:12/76	26 ± 4
4/77	113	4	3.54	4	1	2/77	
5/77	113	6	5.31		1	4/77	
6/77	109	7	6.42	1	1	4/77	37 + 18
7/77	109	5	4.59	4			
8/77	96	2	2.08		1	7/77	
9/77	94	5	5.32		1	7/77	
10/77	278	14	5.04		1	6/77	60 ± 22
11/77	278	6	2.16				
12/77	141	8	5.67				
1/78							
2/78	98	4	4.08				
Totals	2,083	109		14	8		

TABLE 2. MORPHOLOGICAL MEASUREMENTS BY SEX AND AGE CLASS OF NORWAY RATS ON ST. CLEMENTS ISLAND.\*

Age Class	Sex	Sample Size	Weight (GMS.)	Total Length	Body Length	Tail Length	Hind Foot	Ear Length
Juvenile	Male	13	89.6 ( 73.4-105.8)	275.2 (259.1-291.3)	146.2 (137.9-154.5)	129.0 (120.9-137.1)	37.6 (36.6-38.9)	20.8 (19.9-21.7)
	Female	11	113.4 ( 86.9-139.9)	293.4 (272.4-314.4)	156.0 (148.5-168.2)	136.4 (126.3-146.5)	37.7 (36.2-39.2)	21.0 (20.2-21.8)
	Combined	24	100.6 ( 85.9-115.2)	283.5 (270.9-296.0)	151.1 (144.4-156.8)	132.4 (126.3-138.5)	37.7 (36.8-38.6)	20.9 (20.4-21.4)
Subadult	Male	10	213.5 (180.9-237.0)	370.3 (358.4-382.2)	194.6 (187.4-201.8)	175.7 (167.3-184.1)	42.6 (41.0-44.2)	22.2 (20.9-23.4)
	Female	13	186.1 (174.9-192.2)	355.7 (346.1-365.3)	187.0 (182.7-191.3)	168.7 (162.2-175.2)	40.8 (39.7-41.9)	22.6 (21.9-23.3)
	Combined	23	198.0 (185.6-210.4)	362.0 (354.4-369.6)	190.3 (186.3-194.2)	171.7 (166.8-176.7)	41.6 (40.7-42.5)	22.4 (21.8-23.0)
Adult	Male	26	287.1 (258.6-315.6)	402.9 (391.8-413.9)	214.6 (207.7-221.5)	188.4 (183.2-193.6)	44.4 (43.7-45.1)	23.9 (23.4-24.4)
	Female	34	273.1 (254.9-291.3)	399.7 (391.4-408.0)	212.6 (207.9-217.3)	187.1 (182.8-191.2)	41.4 (40.6-42.2)	23.3 (22.6-24.0)
	Combined	60	279.0 (263.5-294.5)	401.1 (394.6-407.6)	213.4 (209.5-217.3)	187.7 (184.5-190.9)	42.7 (42.9-43.4)	23.6 (23.1-24.1)

subadults and juveniles accounted for 21.7 percent and 22.6 percent, respectively. Table 2 presents the mean and 95 percent confidence intervals for the morphological measurements of each age class and sex.

The reproductive organs of fetuses were clearly visible at approximately 15 days after insemination. At that age they had a mean crown rump measurement of 14.4 mm (range 12-18 mm) and a mean weight of 0.698 (range 0.422-0.870). There were no incidences of females possessing active corpora lutea without viable embryos, and, therefore, no fetuses less than 6 days old in the sample (Table 3).

TABLE 3. ESTIMATE OF AGE IN DAYS OF FETUSES OBTAINED FROM PREGNANT FEMALE RATS CAPTURED ON ST. CLEMENTS ISLAND, 1976-78.

RML #	Uterine Condition <sup>a</sup>	Embryos #	Mean Fetal Length (mm)	Mean Fetal Weight (g)	Stage of Gestation (Days)
4	F	8	14.4	0.698	15
12	D	9	<8.0	0.051	6-12
18	C	7	<8.0	<0.05	6-12
28	C	8	<8.0	<0.05	6-12
45	C-D	9	<8.0	<0.05	6-12
48	D-E	9	<8.0	<0.05	6-12
49	D-E	12	<8.0	<0.05	6-12
50	Near Term	11	35.8	5.513	21-25
58	C-D	8	<8.0	<0.05	6-12
59	F	9	8.7	0.10	13
60	C-D	8	<8.0	<0.05	6-12
62	C	8	<8.0	<0.05	6-12
63	Near Term	6	29.5	3.392	20
65	C	5	<8.0	<0.05	6-12
78	D-E	17	<8.0	<0.05	6-12
75	C-D	8	<8.0	<0.05	6-12
80	Near Term	7	22.8	1.676	18
109	C-D	8	<8.0	<0.05	6-12

<sup>a</sup>Uterine condition was compared to illustrations in Emlen and Davis (1948:62). (A) No noticeable change; (B) vague opaqueness at certain points; (C) elongated whitish areas slightly wider than uterine tube; (D) small round nodules about double the width of the uterine horn; (E) uterus has nodular appearance; (F) uterine horn appears tubular; (Near Term) features of fetus can be distinguished.

## REPRODUCTION

## Sex Ratios

The overall sex ratio of 107 Norway rats collected during the study for which the sex could be determined was 84.5 males per 100 females. This sex ratio was not found to differ significantly from a 1:1 ratio. More males than females were found in the juvenile age class, while females were dominant in the subadult and adult level. No significant differences in the sex ratios were found, however, for any age class. Fetal sex ratios showed an abundance of males with a ratio of 113 males per 100 females, not significantly different from a 1:1 ratio (Table 4).

TABLE 4. SEX RATIOS OF FETAL, JUVENILE, SUBADULT AND ADULT NORWAY RATS ON ST. CLEMENTS ISLAND, 1976-1978) (NONE OF THE DIFFERENCES WERE SIGNIFICANT).

Source	Sample Size	Number of Males	Number of Females	Males Per 100 Females
Adults	60	26	34	76.5
Subadults	23	10	13	76.9
Juveniles	24	13	11	118.2
Combined	107	49	58	84.5
Embryonic	32	17	15	113.3
	139	66	73	90.4

In the cases where fetuses could be sexed, male testes and epididymides were located in the posterior section of the body cavity on each side of the urinary bladder. Females fetuses exhibited marked changes in the size and location of the ovaries in relation to the adrenals and kidney. In the youngest fetuses that could be sexed, the ovaries were relatively large and were anterior to the adrenal gland. Near term fetuses had ovaries that were considerably smaller and were found posterior to the kidney. Fetuses between these two developmental stages showed ovaries of a compromising size adjacent to the kidneys (Fig. 6).

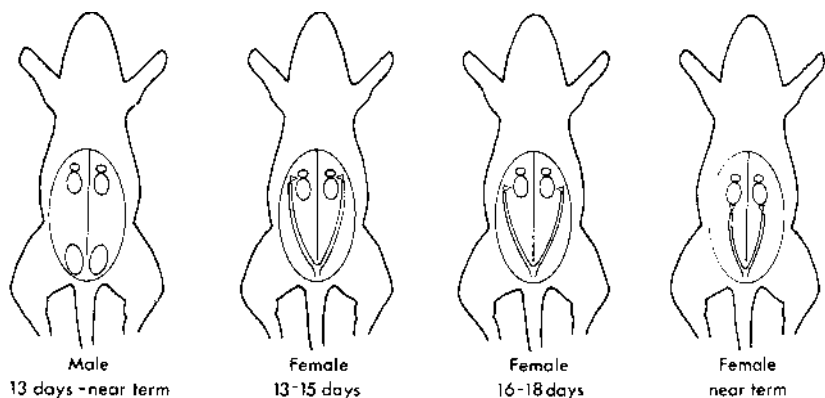


Fig. 6. Relative Position of Fetal Gonads in Male and Female Norway Rats on St. Clements Island (1976-1978).

### Breeding Season

Adult males were reproductively active in all months of the year. Although males were not collected during January, April and July, adjacent months indicate the trend to be consistent (Figs. 7 and 8). Of the 26 adult males examined, only two, one trapped on October and one in November, showed little or no sperm in the testes and epididymides. Conversely, two subadult males captured in May and November had active spermatozoa. No juveniles were reproductively active.

The highest mean monthly testes weight/body weight ratios were found in May and June, and decreased to a low in December (Fig. 8). Testes weight/body weight ratios were positively correlated with the mean monthly temperature ( $r = 0.3313$ ,  $P 0.01$ ,  $df = 48$ ) (Table 5). Adult males showed positive correlations of the testes weight ratio with freeze free days ( $r = 0.4155$ ,  $p 0.017$ ,  $df = 25$ ) and total precipitation ( $r = 0.4531$ ,  $p 0.01$ ,  $df = 25$ ) (Table 6).

Females were visibly pregnant from February through October. By assuming that embryos are macroscopically visible for the last 18 of the 25 day gestation period (Davis 1953:380), and back dating the estimated embryo age, it was determined that conception first occurred on approximately

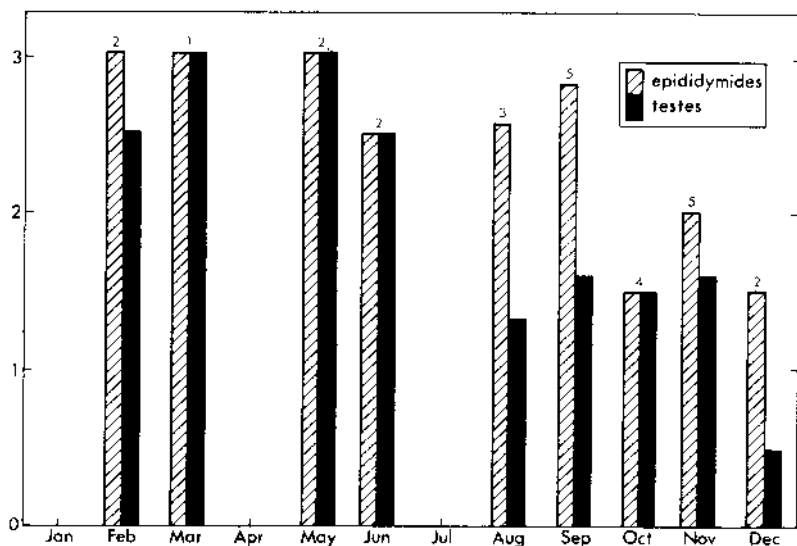


Fig. 7. Mean Monthly Variations in Relative Amounts of Sperm in Adult Male Norway Rats Collected on St. Clements Island (1976-1978).

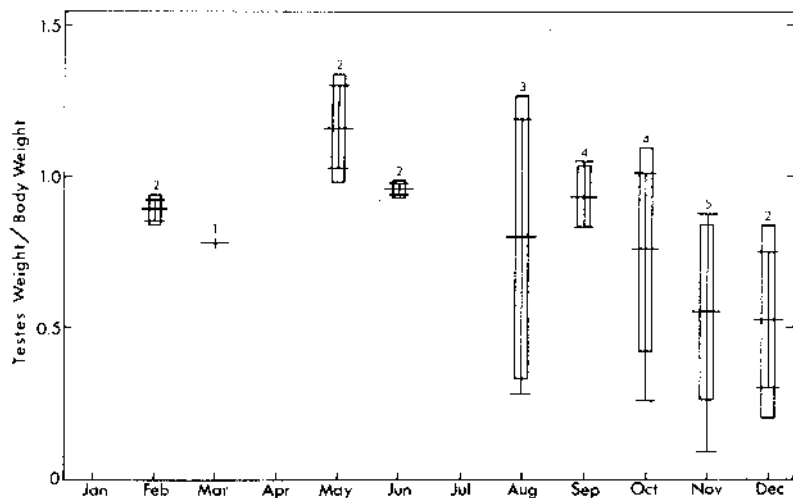


Fig. 8. Distribution of Testes Weight Per Body Weight Ratios by Month for Adult Male Norway Rats Collected on St. Clements Island (1976-1978).

TABLE 6. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF  
 TABLE 5. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF  
 ADULT MALE RATS FROM ST. CLEMENTS ISLAND 1976-78.  
 MALE RATS ON ST. CLEMENTS ISLAND 1976-78.

	1	2	3	4	5	6	7	8	9	10	11
1. Adrenal Index	1.00 (0.000)										
2. Spleen Index	0.0076 (0.480)	1.00 (0.000)									
3. Condition Index	-0.5238 (0.001)	0.2174 (0.071)	1.00 (0.000)								
4. Month	0.3642 (0.005)	0.0026 (0.439)	-0.1191 (0.213)	1.00 (0.000)							
5. Age	-0.4915 (0.001)	0.2847 (0.024)	0.6538 (0.001)	0.2322 (0.054)	1.00 (0.000)						
6. Freeze Free Days	-0.0037 (0.490)	-0.2880 (0.022)	-0.3089 (0.017)	-0.3011 (0.018)	-0.2595 (0.036)	1.00 (0.000)					
7. Mean Temperature	-0.3213 (0.013)	-0.1789 (0.109)	0.0420 (0.390)	-0.6236 (0.001)	0.0554 (0.353)	0.5704 (0.001)	1.00 (0.000)				
8. Total Precipitation	0.2518 (0.042)	0.0279 (0.425)	-0.1749 (0.120)	0.0140 (0.462)	-0.3611 (0.005)	0.3445 (0.008)	0.3043 (0.017)	1.00 (0.000)			
9. Body Fat	0.0210 (0.444)	-0.1513 (0.150)	0.2589 (0.039)	0.1822 (0.105)	0.1855 (0.101)	-0.1817 (0.106)	-0.4061 (0.002)	-0.4250 (0.001)	1.00 (0.000)		
10. K Value	-0.4221 (0.002)	0.2475 (0.047)	0.5008 (0.001)	-0.0658 (0.330)	0.7587 (0.001)	-0.5167 (0.001)	-0.2361 (0.055)	-0.3615 (0.006)	0.2455 (0.048)	1.00 (0.000)	
11. Testes Index	-0.3685 (0.005)	-0.1011 (0.245)	0.3808 (0.004)	-0.5412 (0.001)	0.7144 (0.001)	0.0134 (0.463)	0.3313 (0.010)	-0.0609 (0.339)	0.0365 (0.420)	0.4715 (0.001)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the HoR=O (df from 45 to 48).



TABLE 6. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF ADULT MALE RATS FROM ST. CLEMENTS ISLAND 1976-78.

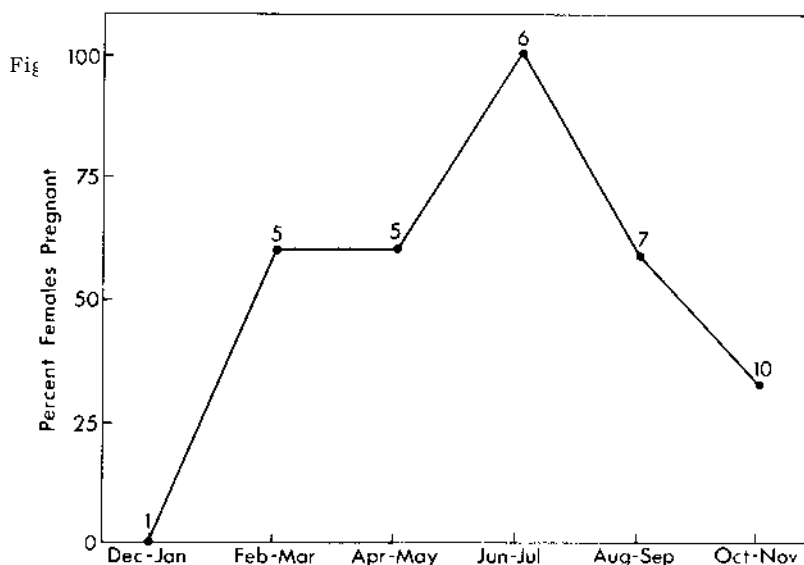
	1	2	3	4	5	6	7	8	9	10	11
1. Adrenal Index	1.00 (0.000)										
2. Spleen Index	0.3538 (0.038)	1.00 (0.000)									
3. Condition Index	-0.2148 (0.157)	-0.1896 (0.187)	1.00 (0.000)								
4. Month	0.2797 (0.083)	0.1457 (0.239)	-0.0700 (0.373)	1.00 (0.000)							
5. Age	- (0.000)	-	-	-	1.00 (0.000)						
6. Freeze Free Days	-0.3552 (0.038)	-0.4371 (0.013)	-0.0830 (0.350)	-0.2314 (0.128)	-	1.00 (0.000)					
7. Mean Temperature	-0.4404 (0.012)	-0.4417 (0.012)	0.2407 (0.129)	-0.3644 (0.034)	-	0.7319 (0.001)	1.00 (0.000)				
8. Total Precipitation	0.0968 (0.319)	0.0553 (0.0394)	-0.1132 (0.299)	0.1834 (0.185)	-	0.4640 (0.008)	0.2819 (0.081)	1.00 (0.000)			
9. Body Fat	0.2824 (.081)	-0.2874 (.077)	0.1372 (.261)	0.1581 (.220)	-	-0.3366 (.046)	-0.3385 (.045)	-0.4797 (.007)	1.00 (.000)		
10. K Value	-.1366 (.262)	-.0805 (.354)	-.0252 (.453)	-.0605 (.389)	-	-.3764 (.035)	-.3938 (.028)	-.3597 (.042)	.4145 (.022)	1.00 (.000)	
11. Testes Index	-.0892 (.332)	-.1166 (.285)	.0539 (.401)	-.5073 (.004)	-	.4155 (.017)	.4579 (.009)	.4531 (.010)	-.2878 (.077)	-.3547 (.045)	1.00 (.000)

Fig. 9. Bi-Monthly Reproductive Status of Adult Female Norway Rats Collected on St. Clements Island (1976-1978).  
 \*Numbers in parentheses are the probability (R) under the H<sub>0</sub>:R=0 (df from 23 to 25).

February 14 and 19 for 1977 and 1978, respectively. Latest conception dates were estimated to occur on October 10 in 1977 and October 3 in 1978. The breeding season, therefore, was approximately 237 days per year.

The peak reproductive activity for females was in June and July (Fig. 9). All adult females examined in these months were visibly pregnant. Reproductive activity decreased from this point, with no activity in winter. Resumed activity occurred in the late winter-early spring, with 60 percent of the adult females visibly pregnant from February to May.

The peak of female reproductive activity followed the peak in male testes weight ratios by one month. Female activity continued for an additional month while the male reproductive condition decreased. The reproductive activity of both sexes then decreased to a low in the winter months. Although there is no data presented for January, reproductive activity was expected to have ceased.



## Litter Size

The mean litter size of adult females was determined from embryo and placental scar counts (Table 7). The mean size of 18 litters, based on embryo counts, was  $8.83 \pm 2.62$ , with a range of 5 to 17. Eight embryos per female were found in 33 percent ( $n = 6$ ) of the sample and 9 embryos per female occurred in 22 percent ( $n = 4$ ) of the sample.

Litter  
Size

TABLE 7. COMPARISON OF VIABLE FETUSES AND PLACENTAL SCARS IN DETERMINING THE LITTER SIZE OF NORWAY RATS OF ST. CLEMENTS ISLAND.

	Viable Fetuses		Placental Scars		Combined	
	Number	Percent	Number	Percent	Number	Percent
1						
2			1	7.7	1	3.2
3						
4						
5	1	5.5			1	3.2
6	1	5.5	1	7.7	2	6.4
7	2	11.1	3	23.1	5	16.1
8	6	33.3	3	23.1	9	29.0
9	4	22.2	1	7.7	5	16.1
10	1	5.5			1	3.2
11	1	5.5			1	3.2
12	1	5.5			1	3.2
13						
14						
15						
16			2	15.4	2	6.4
17	1	5.5	1	7.7	2	6.4
18						
19			1	7.7	1	3.2
20						
Total	18	100	13	100	31	100
Mean	8.83		10.00		9.35	

Conaway (1955:520) found that the appearance of resorption scars were microscopically indistinguishable from those of term scars. Since the total litter loss after implantation is not a common occurrence in the Norway rat (Perry 1945:35), placental scar counts were assumed to be from term pregnancies when found in the absence of viable fetuses. Therefore, placental scars are indicators of the initial litter size. The mean initial litter size of 12 Norway rats exhibiting placental scars was 10.0 per female with a range of 2 to 19. Placental counts of 7 and 8 per female occurred in equal frequencies accounting for 46 percent ( $n = 6$ ) of the sample.

Mean litter size determined from combined fetus and placental scar counts was 9.35 per female with a range of 2 to 19. Sixty-one percent ( $n = 19$ ) of the sample fell into the litter size of 7 to 9.

No seasonal variation in litter size was found utilizing Spearman's Rank Correlation Coefficient ( $r = -0.2926$ ,  $p = 0.11$ ,  $df = 17$ ), although a significant positive correlation was found when comparing litter size with relative body fat ( $r = 0.4321$ ,  $p = 0.037$ ,  $df = 17$ ) and a highly significant correlation was found when compared with the condition index ( $r = 0.7113$ ,  $p = 0.0001$ ,  $df = 17$ ) (Table 8). These correlations indicate that litter size is dependent upon the size and condition of the female, with the larger females in the best condition having the largest litters. Similar findings were reported by Perry (1945:29) and Davis and Hall (1951:11). No seasonal variation in litter size was observed in either of these studies.

### Ovulations, Embryo Locations and Resorptions

The mean ovulation rate, based on corpora lutea counts from 17 pregnant females was 10.39. The highest frequency was 8 corpora lutea for the paired ovaries with a range of 7 to 17 (Table 9).

Analysis of 289 embryos and placental scars revealed that 123 (42.6%) of the implantations occurred in the left uterine horn while 166 (57.4%) occurred in the right. This difference was found to be slightly different ( $p < 0.05$ ) for the two sides.

TABLE 8. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF PREGNANT FEMALE RATS FROM ST. CLEMENTS ISLAND 1976-78.

	1	2	3	4	5	6	7	8	9	10	11	12
1. Adrenal Index	1.00 (0.000)											
2. Spleen Index	0.0931 (0.361)	1.00 (0.000)										
3. Condition Index	-0.2328 (0.184)	-0.0155 (0.476)	1.00 (0.000)									
4. Month	-0.2976 (0.123)	0.1260 (0.309)	0.4137 (0.044)	1.00 (0.000)								
5. Age	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)							
6. Freeze Free Days	-0.3156 (0.109)	0.0932 (0.356)	0.1687 (0.252)	0.7543 (0.001)	- (0.000)	1.00 (0.000)						
7. Mean Temperature	-0.2975 (0.123)	-0.0052 (0.492)	-0.0251 (0.461)	0.3840 (0.058)	- (0.034)	0.4396 (0.000)	1.00 (0.000)					
8. Total Precipitation	-0.1357 (0.302)	0.1014 (0.344)	0.4831 (0.021)	0.7287 (0.001)	- (0.001)	0.7263 (0.107)	0.3072 (0.000)	1.00 (0.000)				
9. Body Fat	-0.0609 (0.408)	-0.2631 (0.146)	-0.0775 (0.380)	-0.0980 (0.349)	- (0.321)	-0.1175 (0.020)	-0.4867 (0.272)	-0.1535 (0.000)	1.00 (0.000)			
10. Resorption Rate	-0.4525 (0.034)	0.0979 (0.350)	0.2128 (0.198)	0.0308 (0.452)	- (0.072)	-0.3580 (0.251)	0.1692 (0.324)	-0.1153 (0.098)	-0.3202 (0.000)	1.00 (0.000)		
11. Litter Size	0.2761 (0.142)	-0.2421 (0.167)	-0.2316 (0.178)	-0.2926 (0.119)	- (0.150)	-0.2587 (0.400)	0.0643 (0.336)	-0.1071 (0.037)	0.4321 (0.283)	-0.1450 (0.000)	1.00 (0.000)	
12. K Value	-0.1291 (0.311)	-0.0145 (0.477)	-0.0341 (0.477)	-0.2048 (0.208)	- (0.098)	-0.3193 (0.465)	-0.0220 (0.236)	-0.1814 (0.168)	0.2402 (0.123)	0.2885 (0.001)	0.7113 (0.000)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the  $H_0: R=0$  (df from 16 to 17).

TABLE 9. MONTHLY OVULATION AND RESORPTION RATES FOR SEXUALLY ACTIVE FEMALE NORWAY RATS ON ST. CLEMENTS ISLAND

<u>Month</u>	<u>Sample Size</u>	<u>Active Corpora Lutea</u>	<u>Viable Fetuses</u>	<u>Number Resorbed</u>	<u>Percent Resorbed</u>
January	—	—	—	—	—
February	2	18	17	1	5.56
March	1	10	9	1	10.00
April	2	27	23	4	14.81
May	1	8	8	0	0
June	5	55	37	18	32.73
July	1	13	17	—4	—
August	0	—	—	—	—
September	4	41	33	8	19.51
October	2	15	15	0	0
November	0	—	—	—	—
December	0	—	—	—	—
Total	18	187	159	28	
Mean		10.39	8.83	—	15.01

Analysis of the relationship between the ovulation rate of 10.39 to the mean litter size of 8.83 showed that 15.0 percent of the ovulated eggs failed to implant or were resorbed (Table 9).

One pregnant adult female captured in July had 9 embryos in the right uterine horn and 8 embryos in the left. When examining histological sections of the ovaries, only 7 active corpora lutea were present in the right ovary and 6 on the left. Twinning, resulting from polyovular follicles would account for this occurrence (Davis and Hall 1950).

Of the 18 litters in the sample, only 2 (11%) showed visible signs of resorption. Although size variations were found within litters, only embryos obviously resorbed were included in the calculation of the resorption rate. One female caught in September 1976 had 3 resorbed embryos in a litter of 11 (27%) while another female captured in June 1976 resorbed 1 embryo in a litter of 10 (10%). From a total of 159 fetuses in 18 litters, only 4 embryos were resorbing for a resorption rate of 2.5 percent. No females were found in which total litter resorption occurred.

## PRODUCTIVITY

The maximum productivity of female Norway rats can be estimated utilizing a modified version of the calculations used for rats in Hawaii by Tamarin and Malecha (1972:524). For this study, productivity (P) is defined as:

$$P = [R(S/G) (L)] - [R(S/G) (L) (m)]$$

where

R = observed pregnancy rate

S = duration of the breeding season

G = gestation period

L = litter size

m = intrauterine mortality

In this study the observed pregnancy rate was 0.53. The breeding season was approximately 237 days. The gestation period was assumed to be 25 days (Davis 1953) and litter size in the sample was 8.83 per female. Intrauterine mortality was estimated at 15.01 percent. From these estimates, the maximum productivity per female per year is 37.7 young from 5 litters.

Davis (1950a:462) described a method of estimating the annual number of young weaned by an adult female. Prevalence, which described the frequency or percent of occurrence, was converted into incidence, defined as the rate of occurrence. The formulas, modified for this study was expressed as:

$$I_p = \frac{t(P)}{g}$$

where

$I_p$  = incidence of pregnancy

t = breeding season

P = prevalence of pregnancy

g = gestation period

and,

$$= \frac{t(L)}{d}$$

where

$I_L$  = incidence of lactation

t = breeding season

L = prevalence of lactation

d = duration of days of lactation

The incidence of pregnancy would approximate the number of litters born whereas the incidence of lactation would estimate the number of litters weaned annually.

By employing these formulas, the incidence of pregnancy of the St. Clements Island rats was estimated to be 5.02.

The mean prevalence of lactation derived from Baltimore rats in various studies was 40.2 (Davis 1953:381) and days of lactation was 36 (Davis 1951a:460). By assuming, these means to be representative of the rats on St. Clements Island, the incidence of lactation was estimated to be 2.65.

The difference between the incidence of pregnancy and lactation gives an estimate of post partum mortality. In this case, an average of 2.37 litters are lost annually per female from the time of mid-pregnancy to the mid-point of lactation. If 2.65 litters were weaned per season by an adult female, and the mean litter size was 8.83, the productivity per adult female was 23.5 young per year.

## PHYSIOLOGICAL RESPONSES

Four morphological indicators were used to determine the degree of physiological response in the Norway rat to environmental changes on St. Clements Island. The indicators were the Condition Index (K), Adrenal Index (AI), Spleen Index (SI) and the Body Fat Index (BFI).

### Condition Index

Analysis of the condition index ( $k$ ) of 105 Norway rats showed no significant differences between the sexes or season (Table 10). Overall seasonal variation was greater for males than females, although a relatively stable response to seasonal changes was indicated for both sexes (Fig. 10). This implies that males and females are in the same general condition throughout the year.

A highly significant difference ( $p < 0.001$ ) was observed between the condition indices of adult and juvenile rats (Table 10). This significance was supported by a positive correlation coefficient ( $r = 0.5883$ ,  $p < 0.001$ ,  $df = 104$ ) for the condition index in relation to age, indicating an increase in the condition of the rat as it matures (Table 11).

Spearman's Rank Correlation Coefficients (Table 11) showed significant differences in the condition index in



TABLE 10. ANALYSIS OF VARIANCE OF SEX, AGE AND SEASON FOR MEAN CONDITION INDICES OF NORWAY RATS ON ST. CLEMENTS ISLAND. SEASONAL PARTITIONS WERE WINTER (DECEMBER-MARCH), SUMMER (APRIL-JULY) AND FALL (AUGUST-NOVEMBER).

Source	df	SS	MS	F	Significance*
Sex	1	0.023	0.023	1.278	NS
Age	1	0.520	0.520	28.889	P < .001
Season	2	0.098	0.049	2.722	NS
Sex x Age	1	0.012	0.012	.667	NS
Sex x Season	2	0.081	0.040	2.222	NS
Age x Season	2	0.046	0.023	1.278	NS
Interaction	2	0.052	0.026	1.444	NS
Error	93	1.693	0.018		
Total	104	2.525			

\*NS = Not Significant

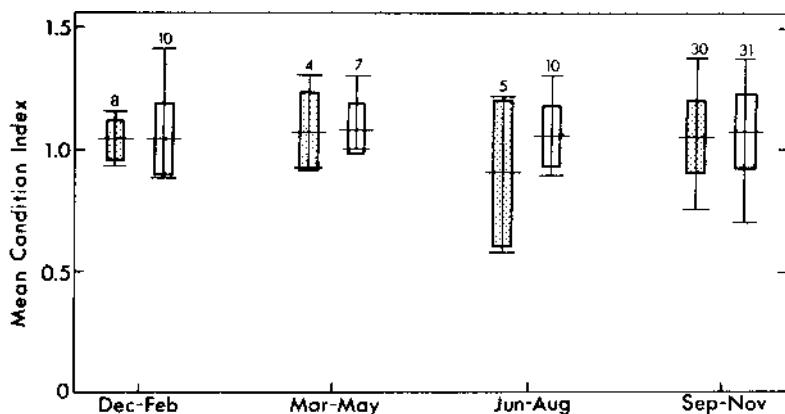


Fig. 10. Combined Seasonal Fluctuations in Mean Condition Indices for Norway Rats Collected on St. Clements Island (1976-1978).

relation to freeze free days. Negative correlations with freeze free days ( $r = -0.1916$ ,  $p = 0.025$ ,  $df = 104$ ) for the population indicate increased weight proportions with the increase of freezing days per month.

TABLE 11. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF MALE AND FEMALE RATS FROM ST. CLEMENTS ISLAND, 1976-78.

	1	2	3	4	5	6	7	8	9	10
1. Adrenal Index	1.00 (0.000)									
2. Spleen Index	0.0237 (0.406)	1.00 (0.000)								
3. Condition Index	-0.4067 (0.001)	0.1426 (0.073)	1.00 (0.000)							
4. Month	0.0227 (0.410)	-0.1524 (0.059)	-0.1859 (0.029)	1.00 (0.000)						
5. Age	-0.1819 (0.032)	0.2120 (0.014)	0.5883 (0.001)	-0.3537 (0.001)	1.00 (0.000)					
6. Freeze Free Days	(0.0567)	-0.1715 (0.039)	-0.1916 (0.025)	-0.2541 (0.004)	-0.1449 (0.068)	1.00 (0.000)				
7. Mean Temperature	-0.1615 (0.051)	0.0131 (0.447)	0.0826 (0.201)	-0.5356 (0.001)	0.0967 (0.161)	0.6471 (0.001)	1.00 (0.000)			
8. Total Precipitation	0.0652 (0.255)	-0.0252 (0.398)	-0.0679 (0.246)	0.0603 (0.269)	-0.2920 (0.001)	0.5215 (0.001)	0.3629 (0.001)	1.00 (0.000)		
9. Body Fat	-0.0103 (0.459)	-0.1842 (0.029)	0.0819 (0.203)	0.3392 (0.001)	0.0258 (0.396)	-0.2521 (0.004)	-0.4839 (0.001)	-0.3461 (0.001)	1.00 (0.000)	
10. K Value	-0.1456 (0.072)	0.1736 (0.038)	0.4738 (0.001)	-0.2607 (0.004)	0.7933 (0.001)	-0.3448 (0.001)	-0.0888 (0.184)	-0.3288 (0.001)	0.1341 (0.086)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the  $H_0: R=0$  (df from 103 to 106).

Mean temperature (Table 12) was also found to be significant when correlated with the condition index of juveniles ( $r = -0.3509$ ,  $p = 0.043$ ,  $df = 24$ ). Total precipitation was found to be significant ( $r = 0.4831$ ,  $p = 0.021$ ,  $df = 17$ ) for the condition index of pregnant females (Table 8). In Table 5 males show correlations of the condition index with body fat ( $r = 0.2589$ ,  $p = 0.039$ ,  $df = 46$ ) and relative testes weight ( $r = 0.3808$ ,  $p = 0.004$ ,  $df = 46$ ).

### Adrenal Index

A difference was observed between the mean adrenal weight of the right and left gland, the latter being significantly larger ( $p < 0.05$ ). Similar findings have been reported for albino rats (H. H. Donaldson 1924:126) and brush rabbits, *Sylvilagus bachmani*, (Chapman 1971:455).

Seasonal fluctuations in the mean adrenal index for male and female Norway rats followed a similar pattern throughout the study. Males had lower indices than females in all seasons and, when partitioned by sex, age and combined seasons was highly significant ( $p < 0.001$ ) (Table 13). Variation between males and females was larger in 1976 than in 1977 and was particularly evident in the winter of 1976-77 (Fig. 11). No significant differences were found when the data were partitioned by sex and season (Table 14).

Peaks in female adrenal indices occurred in the winter of 1976-77 and 1977-78, while a low was recorded in the fall of 1976. No change was apparent from April through November of 1977. Similarly, male rats had a peak in the adrenal index in the winter of 1977-78, a low in the fall of 1976, increasing to a peak in the winter of 1977-78. There was, however, no increase in the index of males for the winter of 1976-77 as seen in the females. Virtually no change in the index occurred from the fall of 1976 to the winter of 1976-77 (Fig. 11).

Spearman's Rank Correlation Coefficients (Table 11) for the sample shows a negative correlation between the adrenal index and age class ( $r = -0.1819$ ,  $p = 0.032$ ,  $df = 103$ ) indicating higher adrenal indices in the lower age classes. Adult rats showed a negative correlation for adrenal indices and mean temperature ( $r = -0.2468$ ,  $p = 0.030$ ,  $df = 58$ )

TABLE 12. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF JUVENILE MALE AND FEMALE RATS FROM ST. CLEMENTS ISLAND, 1976-78.

	1	2	3	4	5	6	7	8	9	10
1. Adrenal Index	1.00 (0.000)									
2. Spleen Index	-0.0843 (0.348)	1.00 (0.000)								
3. Condition Index	-0.3913 (0.029)	0.3900 (0.027)	1.00 (0.000)							
4. Month	-0.0492 (0.410)	-0.1798 (0.195)	0.3428 (0.047)	1.00 (0.000)						
5. Age	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)					
6. Freeze Free Days	0.4217 (0.020)	-0.0422 (0.421)	-0.4162 (0.019)	-0.5530 (0.002)	- (0.000)	1.00 (0.000)				
7. Mean Temperature	0.0636 (0.384)	0.1791 (0.196)	-0.3509 (0.043)	-0.9985 (0.001)	- (0.002)	0.5549 (0.002)	1.00 (0.000)			
8. Total Precipitation	0.2634 (0.107)	-0.3645 (0.037)	-0.1223 (0.280)	-0.1732 (0.204)	- (0.203)	0.4037 (0.249)	0.1422 (0.490)	1.00 (0.000)		
9. Body Fat	0.2818 (0.091)	0.0459 (0.414)	0.3271 (0.055)	0.3481 (0.044)	- (0.050)	0.3372 (0.050)	-0.3365 (0.490)	-0.0055 (0.490)	1.00 (0.000)	
10. K Value	-0.2098 (0.163)	-0.1459 (0.243)	0.3677 (0.035)	0.3718 (0.034)	- (0.004)	-0.5125 (0.038)	-0.3724 (0.038)	-0.1256 (0.275)	0.0275 (0.448)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the  $H_0: R=0$  (df from 24 to 23).

Fig. 11. Seasonal Fluctuations in Mean Adrenal Indices for Norway Rats

Collected on St. Clements Island (1976-1978)

TABLE 13. ANALYSIS OF VARIANCE OF SEX, AGE AND SEASON FOR MEAN ADRENAL INDICES OF NORWAY RATS ON ST. CLEMENTS ISLAND. SEASONAL PARTITIONS WERE WINTER (DECEMBER-MARCH), SUMMER (APRIL-JUNE) AND FALL (AUGUST-NOVEMBER).

Source	df	SS	MS	F	Significance*
Sex	1	14.266	14.266	15.677	P < .001
Age	1	1.426	1.426	1.567	NS
Season	2	3.748	1.874	2.059	NS
Sex x Age	1	2.533	2.533	2.784	NS
Sex x Season	2	0.551	0.276	0.303	NS
Age x Season	2	1.037	0.158	0.569	NS
Interaction	2	0.315	0.158	0.174	NS
Error	91	82.851	0.910		
Total	102	106.727			

\* NS = Not Significant

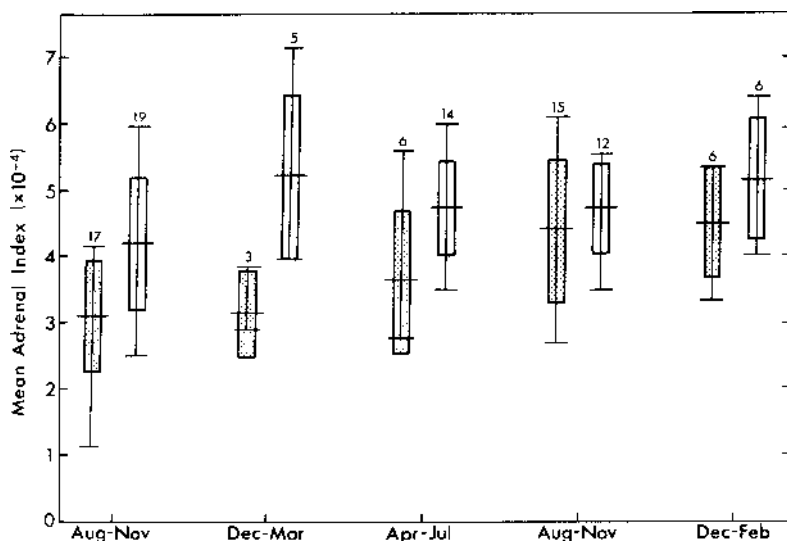


TABLE 14. ANALYSIS OF VARIANCE OF SEX VERSUS SEASON  
FOR MEAN ADRENAL INDICES OF NORWAY RATS  
ON ST. CLEMENTS ISLAND. SEASONAL PARTITIONS  
WERE FALL 1976 (AUGUST-NOVEMBER), WINTER  
1976-77 (DECEMBER-MARCH), SUMMER 1977  
(APRIL-JULY), FALL 1977 (AUGUST-NOVEMBER) AND  
WINTER 1977-78 (DECEMBER-FEBRUARY)

Source	df	SS	MS	F	Significance*
Sex	1	9.495	9.495	0.38	NS
Season	4	3.189	0.797	0.03	NS
Interaction	4	1.554	0.388	0.01	NS
Error	22	546.300	24.832		
Total	31	560.538			

\* NS = Not Significant

(Table 15) while juvenile rats exhibit a positive correlation with freeze free days ( $r = 0.4217$ ,  $p = 0.020$ ,  $df = 23$ ) (Table 12).

Adrenal indices were significantly correlated with the intrauterine mortality rate ( $r = -0.4525$ ,  $p = 0.034$ ,  $df = 16$ ) of pregnant females (Table 8). Non-pregnant females exhibit a positive correlation between the adrenal index and freeze free days ( $r = 0.3145$ ,  $p = 0.026$ ,  $df = 38$ ) (Table 16). Juvenile female adrenal indices were significant when correlated to body fat ( $r = 0.7822$ ,  $p = 0.010$ ,  $df = 10$ ) (Table 17).

Male adrenal indices are significantly correlated to total precipitation ( $r' = 0.2518$ ,  $p = 0.042$ ,  $df = 47$ ) and inversely correlated to mean temperature ( $r = -0.3213$ ,  $p = 0.013$ ,  $df = 47$ ), K value ( $r = 0.4221$ ,  $p = 0.002$ ,  $df = 45$ ) and the testes weight index ( $r = -0.3685$ ,  $p = 0.005$ ,  $df = 48$ ) (Table 5). When partitioned into age classes, adult male adrenal indices were correlated with freeze free days ( $r = -0.3552$ ,  $p = 0.038$ ,  $df = 25$ ) (Table 6), subadult males with body fat ( $r = -0.6755$ ,  $p = 0.023$ ,  $df = 8$ ) (Table 18) and juvenile males with total precipitation ( $r = 0.4942$ ,  $p = 0.043$ ,  $df = 12$ ) (Table 19).

### Spleen Index

The mean spleen index was significantly different for sex and age. Females have significantly higher spleen indices than males ( $p < 0.05$ ), and adults showed higher indices than

TABLE 15. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF ADULT MALE AND FEMALE RATS FROM ST. CLEMENTS ISLAND, 1976-78

	1	2	3	4	5	6	7	8	9	10
1. Adrenal Index	1.00 (0.000)									
2. Spleen Index	0.1990 (0.065)	1.00 (0.000)								
3. Condition Index	-0.2603 (0.025)	-0.1370 (0.153)	1.00 (0.000)							
4. Month	-0.0989 (0.228)	-0.0526 (0.345)	0.0510 (0.352)	1.00 (0.000)						
5. Age	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)					
6. Freeze Free Days	-0.1675 (0.102)	-0.2138 (0.051)	-0.0843 (0.265)	-0.0448 (0.367)	- (0.000)	1.00 (0.000)				
7. Mean Temperature	-0.2468 (0.030)	-0.2072 (0.056)	0.0987 (0.231)	-0.2051 (0.058)	- (0.001)	0.6537 (0.001)	1.00 (0.000)			
8. Total Precipitation	-0.0409 (0.379)	0.0801 (0.272)	0.1315 (0.163)	0.2191 (0.046)	- (0.001)	0.6466 (0.001)	0.4540 (0.001)	1.00 (0.000)		
9. Body Fat	-0.0351 (0.396)	-0.2893 (0.012)	0.1040 (0.219)	0.2798 (0.015)	- (0.005)	-0.3273 (0.001)	-0.4848 (0.001)	-0.4116 (0.001)	1.00 (0.000)	
10. K Value	-0.0494 (0.358)	-0.0745 (0.289)	-0.0111 (0.467)	-0.1680 (0.104)	- (0.002)	-0.3677 (0.002)	-0.2346 (0.038)	-0.3143 (0.008)	0.3173 (0.008)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the  $H_0: R=0$  (df from 56 to 59).

TABLE 16. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF NONPREGNANT FEMALE RATS FROM ST. CLEMENTS ISLAND 1976-78.

	1	2	3	4	5	6	7	8	9	10	11	12
1. Adrenal Index	1.00 (0.000)											
2. Spleen Index	-0.1043 (0.264)	1.00 (0.000)										
3. Condition Index	-0.2563 (0.058)	0.0876 (0.295)	1.00 (0.000)									
4. Month	-0.2337 (0.076)	-0.4284 (0.003)	-0.1295 (0.213)	1.00 (0.000)								
5. Age	0.0898 (0.293)	0.1245 (0.222)	0.4393 (0.002)	-0.2318 (0.75)	1.00 (0.000)							
6. Freeze Free Days	0.3145 (0.026)	-0.0186 (0.455)	-0.1769 (0.137)	-0.4864 (0.001)	-0.1581 (0.165)	1.00 (0.000)						
7. Mean Temperature	-0.0130 (0.469)	0.2674 (0.048)	0.0392 (0.405)	-0.6718 (0.001)	-0.0299 (0.427)	0.8027 (0.001)	1.00 (0.000)					
8. Total Precipitation	0.0733 (0.329)	-0.0855 (0.300)	-0.1224 (0.226)	-0.1338 (0.205)	-0.3471 (0.014)	0.6391 (0.001)	0.4653 (0.001)	1.00 (0.000)				
9. Body Fat	-0.0263 (0.437)	-0.2143 (0.092)	-0.0118 (0.471)	0.5359 (0.001)	-0.0097 (0.476)	-0.3900 (0.006)	-0.5271 (0.001)	-0.4066 (0.005)	1.00 (0.000)			
10. Resorption Rate	-	-	-	-	-	-	-	-	-	1.00 (0.000)		
11. Litter Size	-	-	-	-	-	-	-	-	-	-	1.00 (0.000)	
12. K Value	0.1040 (0.264)	0.1418 (0.191)	0.3161 (0.023)	-0.1008 (0.268)	-0.8251 (0.001)	-0.2926 (0.033)	-0.1717 (0.145)	-0.4080 (0.004)	0.1599 (0.162)	-	-	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the  $H_0: R=0$  (df from 38 to 39).



TABLE 17. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF JUVENILE FEMALE RATS FROM ST. CLEMENTS ISLAND 1976-78.

	1	2	3	4	5	6	7	8	9	10	11	12
1. Adrenal Index	1.00 (0.000)											
2. Spleen Index	-0.3909 (0.117)	1.00 (0.000)										
3. Condition Index	-0.4182 (0.100)	0.3636 (0.136)	1.00 (0.000)									
4. Month	0.2941 (0.190)	-0.4933 (0.062)	-0.1518 (0.328)	1.00 (0.000)								
5. Age	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)							
6. Freeze Free Days	0.3321 (0.159)	-0.1138 (0.369)	-0.3415 (0.152)	-0.5842 (0.030)	- (0.000)	1.00 (0.000)						
7. Mean Temperature	-0.2637 (0.217)	0.4662 (0.074)	0.1130 (0.370)	-0.9927 (0.001)	- (0.000)	0.5799 (0.031)	1.00 (0.000)					
8. Total Precipitation	0.1056 (0.379)	-0.2482 (0.231)	0.1795 (0.299)	0.2204 (0.257)	- (0.000)	0.0882 (0.398)	-0.3228 (0.167)	1.00 (0.000)				
9. Body Fat	0.6822 (0.010)	-0.3518 (0.144)	-0.0959 (0.390)	0.2002 (0.277)	- (0.000)	0.3782 (0.126)	-0.1712 (0.307)	-0.0433 (0.450)	1.00 (0.000)			
10. Resorption Rate	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)		
11. Litter Size	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)	
12. K Value	0.0410 (0.452)	-0.1868 (0.291)	0.3189 (0.170)	0.6157 (0.022)	- (0.000)	-0.5634 (0.036)	-0.5805 (0.031)	-0.1667 (0.312)	0.2244 (0.254)	- (0.000)	- (0.000)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the Ho:R=O (df = 11).

TABLE 18. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITIONS INDICES OF SUBADULT MALE RATS ON ST. CLEMENTS ISLAND, 1976-78.

	1	2	3	4	5	6	7	8	9	10	11
1. Adrenal Index	1.00 (0.000)										
2. Spleen Index	-0.1000 (0.399)	1.00 (0.000)									
3. Condition Index	-0.3333 (0.190)	0.5333 (0.070)	1.00 (0.000)								
4. Month	0.2547 (0.254)	-0.1318 (0.368)	-0.1669 (0.334)	1.00 (0.000)							
5. Age	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)						
6. Freeze Free Days	-0.3015 (0.215)	-0.0355 (0.464)	0.1330 (0.367)	-0.4580 (0.108)	- (0.000)	1.00 (0.000)					
7. Mean Temperature	0.0437 (0.456)	0.4372 (0.120)	0.2623 (0.248)	-0.8111 (0.004)	- (0.299)	1.00 (0.000)					
8. Total Precipitation	0.4110 (0.136)	0.4896 (0.090)	0.1574 (0.343)	-0.3963 (0.145)	- (0.369)	0.8349 (0.003)	1.00 (0.000)				
9. Body Fat	-0.6755 (0.023)	-0.4108 (0.136)	0.1461 (0.354)	0.0144 (0.485)	- (0.383)	-0.1166 (0.276)	-0.2299 (0.107)	-0.4598 (0.000)	1.00 (0.000)		
10. K Value	0.4268 (0.126)	0.2427 (0.265)	-0.1925 (0.310)	0.5381 (0.068)	- (0.003)	-0.8191 (0.190)	-0.3337 (0.482)	-0.0176 (0.252)	-0.2567 (0.000)	1.00 (0.000)	
11. Testes Index	-0.2000 (0.303)	-0.1667 (0.334)	-0.2667 (0.244)	-0.1933 (0.309)	- (0.156)	-0.3813 (0.412)	-0.0874 (0.360)	-0.1399 (0.381)	0.1187 (0.257)	0.2510 (0.257)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the  $H_0: R=0$  (df = 9).

TABLE 19. SPEARMAN'S CORRELATION COEFFICIENTS\* FOR FACTORS AFFECTING CONDITION INDICES OF JUVENILE MALE RATS ON ST. CLEMENTS ISLAND 1976-78.

	1	2	3	4	5	6	7	8	9	10	11
1. Adrenal Index	1.00 (0.000)										
2. Spleen Index	0.0934 (0.381)	1.00 (0.000)									
3. Condition Index	-0.4780 (0.049)	0.2308 (0.214)	1.00 (0.000)								
4. Month	-0.3169 (0.146)	0.0293 (0.460)	0.7029 (0.003)	1.00 (0.000)							
5. Age	- (0.000)	- (0.000)	- (0.000)	- (0.000)	1.00 (0.000)						
6. Freeze Free Days	0.4001 (0.008)	0.1489 (0.306)	-0.2647 (0.180)	0.5971 (0.012)	- (0.000)	1.00 (0.000)					
7. Mean Temperature	0.3169 (0.146)	-0.0293 (0.460)	-0.7029 (0.003)	-1.0000 (0.001)	- (0.000)	0.5971 (0.012)	1.00 (0.000)				
8. Total Precipitation	0.4942 (0.043)	-0.5515 (0.020)	-0.3089 (0.141)	-0.4685 (0.046)	- (0.000)	0.5917 (0.013)	0.4685 (0.046)	1.00 (0.000)			
9. Body Fat	-0.0135 (0.483)	0.3277 (0.126)	0.6761 (0.004)	0.4505 (0.053)	- (0.000)	0.3198 (0.133)	-0.4505 (0.053)	0.000 (0.500)	1.00 (0.000)		
10. K Value	-0.4319 (0.070)	-0.2423 (0.202)	0.2048 (0.241)	0.0917 (0.378)	- (0.000)	-0.4933 (0.037)	-0.0917 (0.378)	0.0069 (0.491)	0.2202 (0.225)	1.00 (0.000)	
11. Testes Index	0.4451 (0.064)	-0.0330 (0.455)	-0.7143 (0.002)	-0.8639 (0.001)	- (0.000)	0.5846 (0.014)	0.8639 (0.001)	0.5240 (0.027)	-0.2392 (0.205)	-0.0198 (0.473)	1.00 (0.000)

\*Numbers in parenthesis are the probability (R) under the  $H_0: R=0$  (df from 12 to 13).

juveniles ( $p < 0.005$ ). However, no significant interaction between sex and age was found. Consequently, it cannot be assumed that adult females exhibit higher indices than adult males. There were no significant differences in the spleen index when tested by season. There was, however, a significant difference for the interaction of age and season ( $p < 0.05$ ). Further analysis showed adults and subadults to have significantly higher spleen indices in the winter (Table 20). Spleen index trends were highest in the winter and fall, decreased in the spring, and was the lowest in the summer (Fig. 12).

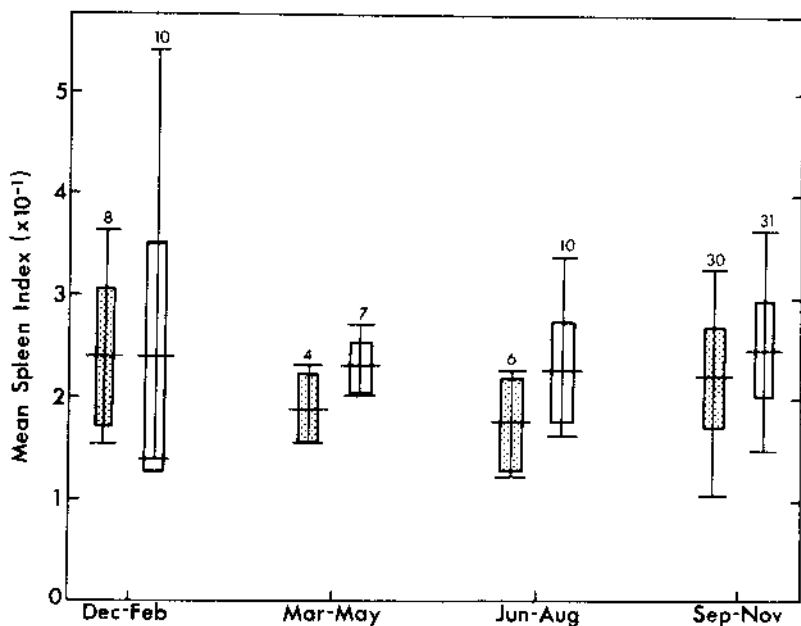


Fig. 12. Combined Seasonal Fluctuations in Mean Spleen Indices for Norway Rats Collected on St. Clements Island (1976-1978).

Spearman's Rank Correlation Coefficient for spleen indices showed positive correlations with age ( $r = 0.2120$ ,  $p = 0.014$ ,  $df = 106$ ) and the K value ( $r = 0.1736$ ,  $p = 0.036$ ,  $df = 104$ ). There was a significant negative correlation between spleen indices with freeze free days ( $r = -0.1715$ ,  $p = 0.039$ ,

TABLE 20. ANALYSIS OF VARIANCE OF SEX, AGE AND SEASON FOR MEAN SPLEEN INDICES OF NORWAY RATS ON ST. CLEMENTS ISLAND. SEASONAL PARTITIONS WERE WINTER (DECEMBER-MARCH), SUMMER (APRIL-JULY) AND FALL (AUGUST-NOVEMBER).

Source	df	SS	MS	F	Significance*
Sex	1	1.582	1.582	5.238	P < .05
Age	1	1.982	1.982	6.563	P < .05
Season	2	0.800	0.400	1.324	NS
Sex x Age	2	0.348	0.348	1.152	NS
Sex x Season	2	0.724	0.362	1.199	NS
Age x Season	2	2.585	1.292	4.278	P < .05
Interaction	2	0.446	0.223	0.738	NS
Error	94	28.385	0.302		
Total	105	36.852			
Simple Main Effects					
Age x Winter	1	9.018	9.018	29.861	< .001
Age x Summer	1	0.110	0.110	0.364	NS
Age x Fall	1	0.012	0.012	0.040	< .05
Adult x Season	2	2.313	1.156	3.828	< .05
Juvenile x Season	2	4.456	2.228	7.377	< .05

\* NS = Not Significant

df = 106) and body fat ( $r = -0.1842$ ,  $p = 0.029$ ,  $df = 106$ ) (Table 11). Juvenile rats had an inverse correlation of spleen indices with total precipitation  $r = -0.3645$ ,  $p = 0.037$ ,  $df = 24$ ) (Table 12).

Non-pregnant females had a positive relationship to mean temperature ( $r = 0.2674$ ,  $p = 0.048$ ,  $df = 39$ ) (Table 16). Pregnant females did not show any significant correlations with the spleen index and any other variable tested (Table 8).

Adult males had a negative correlation of spleen index with mean temperature ( $r = -0.4417$ ,  $p = 0.012$ ,  $df = 25$ ) (Table 6). No additional correlations were observed in males for any age class.

#### Body Fat Index

No significant differences of the body fat index (BFI) was found between the sexes or for any age class. The mean body

fat index however, exhibited a significant difference among seasons ( $p < 0.05$ ) (Table 21). Further analysis revealed a significant drop in the body fat index from winter to summer ( $p < 0.05$ ) followed by a significant increase from summer to fall ( $p < 0.05$ ) (Table 22).

TABLE 21. ANALYSIS OF VARIANCE OF SEX, AGE AND SEASON FOR MEAN BODY FAT INDICES OF NORWAY RATS ON CLEMENTS ISLAND. SEASONAL PARTITIONS WERE WINTER (DECEMBER-MARCH), SUMMER (APRIL-JULY) AND FALL (AUGUST-NOVEMBER).

Source	df	SS	MS	F	Significance*
Sex	1	0.006	0.006	0.009	NS
Age	1	0.691	0.691	1.031	NS
Season	2	4.395	2.198	3.280	$P < .05$
Sex x Age	1	0.964	0.964	1.439	NS
Sex x Season	2	0.110	0.055	0.082	NS
Age x Season	2	0.639	0.320	0.478	NS
Interaction	2	0.842	0.421	0.628	NS
Error	95	63.673	0.670		
Total	106	71.320			

\* NS = Not Significant

TABLE 22.

DUNCAN'S NEW MULTIPLE RANGE TEST FOR SEASONAL VARIATION IN MEAN BODY FAT INDICES FOR NORWAY RATS ON ST. CLEMENTS ISLAND.

	d	LSR	Significance
April-July	$8.059 - 6.204 = 1.855$	$> 0.445$	$P < .05$
August-November	$8.533 - 8.059 = 0.474$	$> 0.445$	$P < .05$
December-March	$8.533 - 6.204 = 2.329$	$> 0.469$	$P < .05$

Seasonal body fat curves show similar fluctuations for male and female rats until the summer of 1977. Body fat curves then diverge slightly until the fall of 1977, and were parallel through the winter of 1977-78 (Fig. 13). Analysis of combined seasonal body fat indices also showed similar patterns for males and females. Females had lower body fat

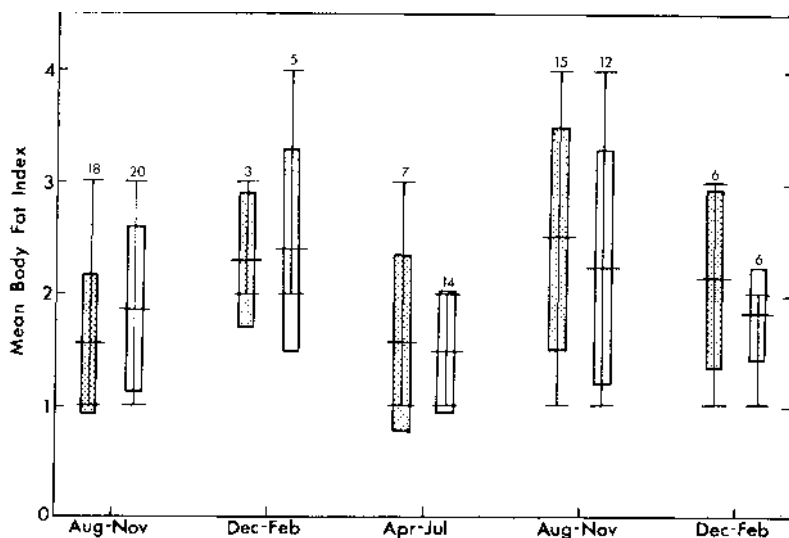


Fig. 13. Seasonal Fluctuations in Mean Body Fat Indices for Norway Rats Collected on St. Clements Island (1976-1978).

indices in all seasons except the fall, although this difference was not found to be significant. Body fat indices peaked for both sexes in the winter and fall. Body fat indices decreased from winter to spring for both sexes. They continued to decrease in females and gradually increased for males from spring to summer. Body fat indices rose sharply from the summer to the fall in females with a slight increase in males (Fig. 14).

Spearman's Rank Correlation analysis for the composite sample (Table 11) showed negative correlations for the body fat index with freeze free days ( $r = -0.2521$ ,  $p = 0.004$ ,  $df = 106$ ) and mean temperature ( $r = -0.4839$ ,  $p = 0.001$ ,  $df = 106$ ). Total precipitation was significant ( $r = -0.3461$ ,  $p = 0.001$ ,  $df = 106$ ) when correlated with the body fat index for both sexes and all age classes except juveniles (Tables 11 and 12). Pregnant female rats expressed a significant positive correlation of the body fat index with litter size ( $r = 0.4321$ ,  $p = 0.037$ ,  $df = 17$ ) (Table 8).

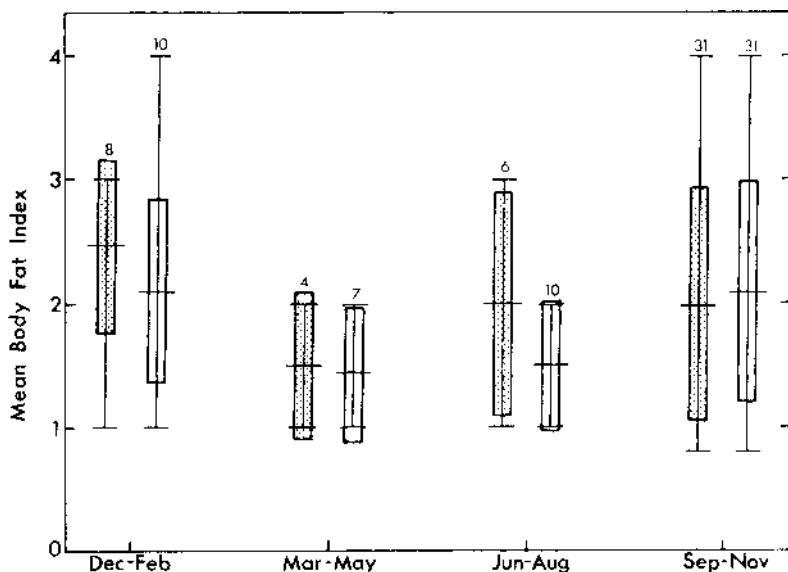


Fig. 14. Combined Seasonal Fluctuations in Mean Body Fat Indices for Norway Rats Collected on St. Clements Island (1976-1978).

### Index Interrelationships

Index interrelationships for the composite sample showed a highly significant negative correlation for the adrenal index and the condition index ( $r = 0.4067$ ,  $p < 0.001$ ,  $df = 101$ ) (Table 11). This relationship was found for both sexes and all age classes. A significant negative correlation of the spleen index and the body fat index ( $r = 0.1842$ ,  $p < 0.029$ ,  $df = 106$ ) was found in adults (Table 15) while juveniles showed a positive correlation of the spleen index and the condition index ( $r = 0.3900$ ,  $p < 0.027$ ,  $df = 24$ ) (Table 12).

Pregnant females showed no significant correlations with any of the variables tested. Males, however, did show a positive correlation of the condition index and the body fat index ( $r = 0.2589$ ,  $p < 0.039$ ,  $df = 46$ ) (Table 5). Adrenal indices were positively correlated with the spleen index of adult males ( $r = 0.3538$ ,  $p < 0.038$ ,  $df = 25$ ), and negatively correlated to the body fat index of subadult males ( $r = -0.6755$ ,  $p < 0.023$ ,  $df = 8$ ) (Tables 6 and 18).



A relationship can be seen among the adrenal, spleen and body fat indices when the seasons were combined over the study period (Fig. 15). The three indices decrease from

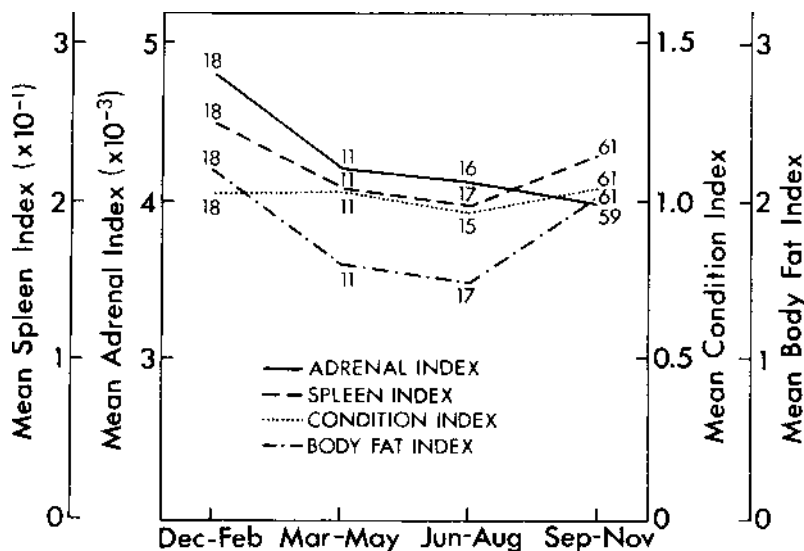


Fig. 15. Comparison of Combined Seasonal Variations in Mean Adrenal Indices (AI), Mean Spleen Indices (SI), Mean Condition Indices (CI) and Mean Body Fat Indices (BFI) for Norway Rats Collected on St. Clements Island (1976-1978).

winter to spring, and slightly decrease from spring to summer. An increase in the spleen and condition index was seen from summer to fall, while the adrenal index continued to decrease. No apparent interrelationships were identified when the four indices were examined by season over the study period (Fig. 16). Adrenal and spleen indices were higher in the winter of 1977-78 than the winter of 1976-77 while the condition and body fat indices were slightly lower.

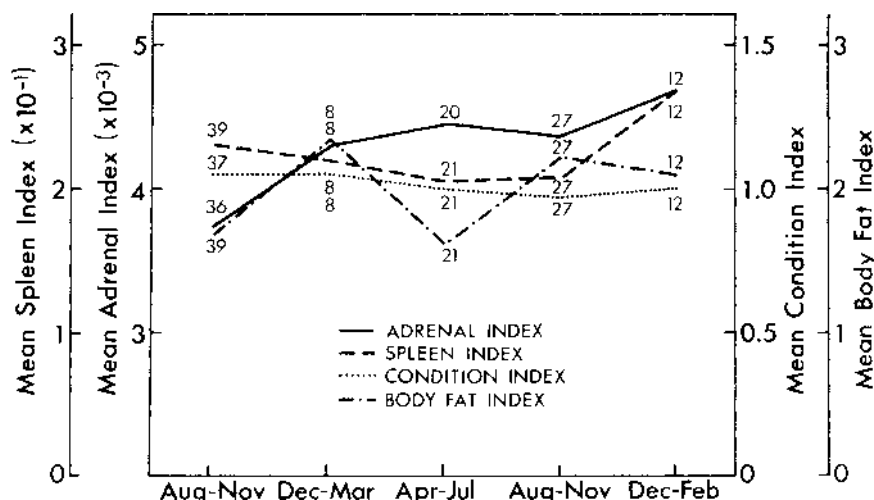


Fig. 16. Comparison of Seasonal Variations in Mean Adrenal Indices (AI), Mean Spleen Indices (SI), Mean Condition Indices (CI) and Mean Body Fat Indices (BFI) for Norway Rats Collected on St. Clements Island (1976-1978).

#### DISCUSSION AND CONCLUSIONS

The reproductive characteristics of wild Norway rats on St. Clements Island are generally similar to those of rat populations found throughout the world. Nonetheless, variations exist which likely reflect the environmental and density differences observed between urban and rural wild rat populations.

Urban rats appear to have adapted to the relatively stable environment in which they exist. Ample harborage is found throughout the year in and around buildings, trash piles and fences (Christian and Davis 1956:476). Food supplies from trash and garbage are usually in excess (Schein and Orgain 1953) with little seasonal variation (Christian and Davis 1956:476). Climatic extremes, with which rural populations must contend, are buffered by the availability of heated human dwellings. Responding to the spatial distribution of their food and harborage, urban rats tend to con-

gregate in localized areas and movement between these areas are minimal (Davis et al. 1948). As a result of these favorable conditions, high densities of urban rats can occur.

Conversely, populations of rural rats tend to be dispersed and dependent upon the distribution of food and harborage. The availability of these necessities can vary with changes in climatic and environmental conditions, necessitating constant relocation and exposure for survival. Consequently, field-living rural populations exhibit lower densities.

Christian (1955; 1956) demonstrated a density dependent adrenocortical response to changes in the population density of laboratory mice. At higher densities, sociopsychological stress, regardless of adequate environmental necessities, resulted in the hypertrophy of the adrenal glands and a consequent reduction in reproductive function. When reproduction was suppressed to the point where mortality surpassed natality, a population decline ensued. Urban Norway rats in Baltimore, Maryland, were studied to determine if this relationship between adrenal hypertrophy and population density holds true under natural conditions (Christian and Davis 1956). Results of this study support the hypothesis of a density dependent mechanism in urban rat population regulation. Sharp population declines in urban rats would, therefore, be expected to occur after reaching peak densities irrespective of seasonal changes.

Rural rat population regulation, however, seems to be influenced to a large degree by climatic, rather than density dependent factors. Norway rats living outside of man-made structures in Nome, Alaska, exhibited heavy mortality in the winter (Schiller 1956:182). Although food and cover were available in dumps, and presumably in sufficient quantity, extremes in temperature produced a drastic reduction on the outdoor population. Rats then obtained harborage in heated buildings, however, and had little trouble surviving the winter. Similar observations were reported by Errington (1934) in a rat population in Wisconsin. Although field wintering rats were concentrated in areas providing adequate food sources, the population was reduced to a minimum, while survival was high for rats finding refuge in man-made structures.

These differences between urban and rural wild Norway rats may suggest different mechanisms controlling rat populations—one in which high population densities inhibit reproductive function causing population decreases irrespective of season, and another in which climatic extremes reduce population levels at particular times of the year. In the low density St. Clements population, we would expect the latter mechanism to exert a greater effect.

Factors in population regulation, however, are not totally independent. The effects of density and climatic conditions vary in magnitude depending on localized extremes. Thus, synergistic effects of various degrees could be expected in population control. A combined effect was seen in two species of Hawaiian rats (*R. rattus* and *R. exulans*) (Tamarin and Malecha 1971:393). The tropical climate varied only slightly and was not expected to have significant effects on population regulation. Density dependent regulation, however, was manifested in the breeding and density cycles of these rodents. Reproduction began when densities were low and ceased in the winter when densities were at a peak. After a short, inactive period, reproductive activity commenced as the density declined. A decrease in reproductive activity when densities were low in the following year also suggested environmental regulation (Tamarin and Malecha 1972:525).

#### POPULATION AND REPRODUCTIVE PARAMETERS

Urban versus rural rat densities indicate high density population control mechanisms in urban rats as compared to climatic control mechanisms in low density rural rat populations. Although urban rat densities are expected to be much higher than those of rural populations (Twigg 1975:59), a direct comparison is not possible. Urban densities have generally been measured as the number per dwelling unit (Davis 1950b) or per city block (Davis 1953:374; Davis and Christian 1958). Other studies of urban Norway rats have measured increasing, stationary and decreasing population levels (Davis 1951b, c; Christian and Davis 1956). These studies, however, indicate high density urban populations as compared to rural rat populations.

A comparison of the St. Clements Island population with other rural rat populations establishes that the maximum estimate of 3.3 rats per ha (1.5 rats per acre) on St. Clements Island was a low density situation. Wirtz (1972:446) reported a mean of 111.2 *R. exulans* per ha (45.0 per acre) while Tomich (1970:200) estimated maximum densities of *R. exulans* and *R. rattus* at 29.6 per ha (12.0 per acre) and 24.7 per ha (10 per acre), respectively. Baker (1946:407) reported maximum densities of 20.8 rats per ha (8.4 per acre) for *R. exulans* and 28.7 rats per ha (11.6 per acre) for *R. mindanesis* in Guam, where the species are sympatric.

The relative abundance, measured in trap success, indicated that the rat density on St. Clements Island had not reached its former carrying capacity. Figure 5 shows the highest relative density at the initiation of the study. The combination of trapping pressure and the effects of the winter of 1976-77 resulted in a sharp decline in rat numbers. The relative density then fluctuated in response to the breeding season, although never exceeding 50 percent of the initial abundance estimate. In addition, the winter of 1977-78 showed a mean abundance increase of 44 percent over the winter of 1976-77 despite similar climatic conditions. A 44 percent yearly increase would approximate a 3.7 percent monthly increase in abundance. Emlen et al. (1948:141) reported that rat populations reduced by 50-90 percent of the carrying capacity increased at a rate of 4 percent per month. Since the relative density on St. Clements Island was low compared to the initial density, and population growth was approximately 4 percent per month, it appears that the population had not exploited the habitat to its maximum, and was increasing.

Density fluctuations in high density urban rat populations are not expected to be seasonally predictable due to the relatively constant environmental and climatic influence. Considerable variation among rat population densities in Baltimore city blocks was shown over a number of years (Davis 1953:375). Rural populations, however, exposed to changing environmental and climatic factors, would be expected to show similar seasonal fluctuations. This was found to be the case for the St. Clements Island population when compared to a rural population of rats on a Maryland farm

(Davis 1953:376). The seasonal density fluctuations coincided with and differed only in magnitude between the two populations. Density peaks, which occurred in March, June, September and December, are related to the breeding season. The March peak was likely due to the increased activity associated with the beginning of the breeding season (Calhoun 1963:113), and resultant increased trap success (Sarrazin and Bider 1973). The increasing density through June coincides with the emergence of juveniles from the first litters conceived in early February. Similarly, December coincides with the emergence of juveniles from the last litters in October, while density increases in September may be attributable to the emergence of juveniles from rats in their first pregnancy.

The breeding season of urban and rural rats are also expected to be different. Davis and Hall (1948; 1951) found that urban rats in Baltimore breed throughout the year with smaller females breeding in two seasons, resulting in a bimodal curve in the prevalence of pregnancy. Although sexually active males on St. Clements Island were evident in all seasons, females were sexually active for 237 days per year (range 236-238). A single peak occurred in the summer, declined in the fall and terminated in the early winter. Female sexual activity did not resume again until early spring. A similar trend was observed in rural Norway rats in the British Isles, in which an anestrus period was evident in winter and a single peak in the prevalence of pregnancy occurred in the spring. Winter cessation of breeding was also reported in penned, outdoor Norway rats by Calhoun (1963:160) and Andrews et al. (1972:162). The initiation of breeding on St. Clements Island was found to occur on February 14 and 19 for the 1976-77 and 1977-78 breeding seasons, respectively. Calhoun (1963:114) reported February 13 as the beginning of breeding in Maryland outdoor rats.

A comparison of litter size between urban and rural Norway rats in Baltimore showed significant differences between the two populations (Davis 1951a:475). Urban rats averaged 10.1 embryos while rural rats had a mean of 8.2 embryos per litter. Differences between the two populations were related to diet. This infers that urban rats, supplied with adequate and consistent amounts and quality of food

can attain larger sizes and consequently larger litters, thus showing higher reproductive potentials and higher densities than are found in comparable rural rats.

The mean litter size (8.83) of St. Clements Island rats was lower than that reported for urban rats and slightly higher than that of rural rats in Baltimore. Davis and Hall (1951:13) reported the mean litter size of 105 urban Norway rats to be 9.83 embryos per litter. The mean litter size of different population levels of urban Norway rats in Baltimore was 10.19 embryos per litter (Davis 1951b:460). The lower litter size of St. Clements Island rats as compared to urban rats was consistent with the findings of Davis (1951a:475) for urban and rural rats.

The mean ovulation rate of 10.39 per female on St. Clements Island was somewhat lower than that reported for urban rats in Baltimore (Hall and Davis 1950:579) and virtually the same as that reported for urban rats in Europe (Perry 1945:32). European rats had a mean of 10.4 while rats in Baltimore had a mean of 11.2 active corpora lutea per pregnant female. Calculations of intrauterine mortality from these three studies revealed rates of 15.0 percent, 15.8 percent and 16.7 percent for the St. Clements, Baltimore and European rats, respectively.

Higher rates of intrauterine mortality would be expected of a population at high densities. Increased competition and stress would lower the reproductive rate by increasing mortality whereas intrauterine mortality in the low density St. Clements Island population would be expected to be less than urban rats.

The percentage of females on St. Clements Island with resorbed embryos as well as the actual resorption rate was lower than that reported for urban rats. Only 11 percent of the pregnant females possessed resorbing embryos and the sample showed a resorption rate of 2.5 percent. Pregnant females in urban habitats, with at least one resorbing embryo, comprised 23 percent of the sample and had a 6 percent resorption rate (Davis and Hall 1951:14).

Annual productivity of the St. Clements Island population was estimated to be 23.5 young per adult female. This rate is low when compared to rates given in the literature per-

taining to productivity of urban Norway rats. Eaton and Stirrett (1928:556) estimated 3 to 4 litters per year in Massachusetts. Although the mean litter size is not reported, applying the worldwide estimate of 8.7 embryos per pregnant female (Davis 1951d:2) gives an average of 25 to 35 offspring per female per year. Emlen and Davis (1948:64) calculated the annual productivity of urban Baltimore rats at 50.3 young per adult female. Annual productivity rates based on various age criterion ranged from 44.4 to 78.9 for urban rats in a poultry warehouse (Davis and Hall 1951:14).

It is not surprising that productivity of rats on St. Clements Island is considerably less than that of urban rats. Urban rats attain sexual maturity at a smaller size and grow to larger sizes than rural populations (Davis 1951a:475). Larger adult females in urban populations would, therefore, exhibit higher incidences of pregnancy and lactation (Davis 1951a:474), higher ovulation rates and larger litters (Perry 1945:29; Davis 1953:386) than comparable rural populations. These differences are shown in the comparative study between rural and urban rats on Baltimore (Davis 1951a). Annual productivity in the city was 35.0 young per female while rural rat productivity was 13.6 young per female. Consequently, urban rats attain high densities in short time periods. At that rate, population levels would soon reach insurmountable proportions without regulation by density dependent controls. Conversely, rural populations do not attain these high densities, and climatic influences apparently regulated survival and consequently population levels.

The population parameters of St. Clements Island rats resemble closely that of the Baltimore farm population. Mean and greatest weight, litter size, breeding season as well as density fluctuations and peaks are similar for the two populations. The differences observed in the productivity of St. Clements Island and farm rats in Baltimore are due to a difference in the prevalence of pregnancy. The St. Clements Island population had a 53 percent prevalence while the farm rats had a 21 percent prevalence of pregnancy. The higher percentage of pregnant females on St.



Clements Island may be related to the increasing population. Davis (1951b:460) has observed significantly higher pregnancy rates in increasing population levels as compared to a stationary level.

#### PHYSIOLOGICAL RESPONSES

Adult Norway rats on St. Clements Island had higher condition indices than juveniles. This may be related to the social conditioning of juvenile rats. Calhoun (1963:148) observed antagonistic behavior of adults towards juveniles. The increased stress during this period of adjustment of social hierarchy may have an effect on physical condition. Davis and Christian (1957) showed a negative relationship between social rank and stress. Christian (1963b:264) reported that voles introduced to a cage containing resident voles exhibited higher levels of stress and showed a reduction in body weight. A reduction in the body weight of low socially ranked juveniles would consequently reduce the condition index value.

A relatively stable condition index was observed throughout the year on St. Clements Island. Davis and Hall (1951:10) found a stable condition index in female Norway rats in Baltimore. The Baltimore population, however, exhibited a striking low during the June through August sampling period. The St. Clements population was also at a low during these months, although the variation was slight. The physical exertion of reproductive activity at its peak may have caused this depression in the condition index.

Sexual dimorphism in the weight of the adrenal gland was seen in the adrenal indices of rats on St. Clements Island. Heavier female adrenal weights have been reported in the cotton rat, *Sigmodon hispidus* (Goertz 1965:699), house mouse, *Mus musculus* (Lidicker 1966:42), Indian mongoose, *Herpestes auropunctatus* (Tomich 1965:239), and others. Adrenocorticoid levels, and alternative index to adrenal weights in many stress studies, has been found to be higher in female Norway rats (Andrews et al. 1972:155) and swamp rats, *R. fuscipes* (Barnett 1977:118), than males. In general, sexual dimorphism in the favor of females is well known and regarded as a "morpho-physiological standard" (Shvarts 1975:135), which is probably related to the breeding

season and reproductive activity (Goertz 1965:699).

Similarly, juveniles are known to exhibit higher degrees of adrenal hypertrophy than adults (Andrews et al. 1972:155). The negative correlation of adrenal indices with age class implies this relationship in the St. Clements population. The tendency of larger animals to be dominant over juveniles (Calhoun 1963:177) would elicit higher states of social stress in the small animals and result in higher adrenal weights (Christian 1963b:267).

Seasonal changes were not significant in the adrenal indices of St. Clements Island rats, although fluctuations were similar to other populations. Adrenal indices peaked in the winter on St. Clements Island. Similar peaks in hyperadrenalism in winter months were reported by Andrews et al. (1972:161) for expanding and saturated populations of Norway rats. It may be that colder weather and shorter days result in adrenal hypertrophy due to winter stress. Lidicker (1966:42) reported significantly larger adrenals in the house mouse due to cold stress. Significantly heavier adrenal indices have also been reported for *S. floridanus* (Chapman et al. 1977) and *Myocastor coypus* (Willner et al. 1979), due to winter stress.

The simultaneous study of the eastern cottontail population on St. Clements Island (Bittner and Chapman in press) allowed us to observe the responses of rodents and lagomorphs to identical climatic conditions under a confined situation. While it was not possible to compare directly the numerical values of the physiological responses of the Norway rats and the eastern cottontails occupying St. Clements Island, a comparison of their general responses to climatic and physiological stresses are of interest.

When the adrenal indices of the St. Clements Island rats were compared with the St. Clements Island *S. floridanus* (Bittner and Chapman in press), a difference was observed. The peak (Fig. 17) in the male *S. floridanus* adrenal indices occurred during the breeding season (January to June) while the peak of the adrenal index in the male Norway rats occurred in the late fall during a period of inclement weather (October to December). Thus, it appeared that, for male *S. floridanus*, breeding and the accompanying domi-

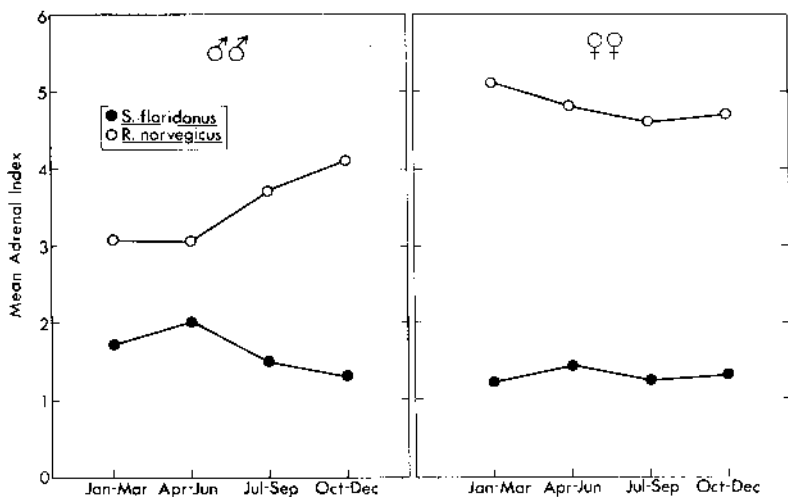


Fig. 17. Comparison of Seasonal Fluctuations in Mean Adrenal Indices of Norway Rats and Eastern Cottontail Rabbits (Bittner and Chapman in press) Collected on St. Clements Island (1976-1978).

nance hierarchy (Marsden and Holler 1964), were more stressful than the adverse climate encountered during winter. Conversely, adverse weather appeared to dominate the adrenal responses of the male Norway rats. The females of both species had similarly shaped adrenal index curves (Fig. 17).

Christian (1963b:304) reported that climate conditions are relatively unimportant in soliciting adrenal responses as compared to density factors in voles. If this were true for the St. Clements population, the peak in adrenal indices would be expected to occur in the summer when population densities peaked and reproductive activity was greatest. However, since the density on St. Clements Island was not considered high and adrenal indices peaked in the winter regardless of the density, climatic conditions were probably responsible for the fluctuations observed.

Splenic indices exhibited the same tendency as the adrenal indices, in that heavier weights were associated

with females. The reverse of the findings for adrenal indices was apparent when juveniles and adults were compared. Whereas juveniles had heavier adrenal indices, they conversely had lower splenic indices.

Splenic indices were highest in the winter and lowest in the summer. The low density on St. Clements Island and the high spleen index during the winter months indicate that climatic conditions were probably responsible for these fluctuations.

The body fat index was found to be highest in the fall and winter months and lowest in the spring and summer. The decrease in body fat from winter to summer and subsequent increase in the fall is similar to the trend observed in the California ground squirrel (Tomich 1962:224) and the house mouse (Lidicker 1966:41). High winter fat indices are also seen in the meadow vole and beach vole, *Microtus breweri*, (Tamarin 1977:543).

Again comparing the Norway rats and eastern cottontails on St. Clements Island (Bittner and Chapman in press), it was found that both species showed similarities in the shape of their body fat index curves (Fig. 18). The only noticeable difference occurred between the males of the 2 species, with the male rabbits having a much lower body fat index than the male rats in the period April to June (Fig. 18). Comparison of the mean condition indices of the Norway rats and cottontails showed that the female rats maintained a constant condition while the female rabbits had a rapid decline in condition for the period April to December (Fig. 19).

Comparison of combined seasonal variation in the physiological responses of the composite sample showed similar trends in the adrenal, spleen and body fat indices. Peaks in adrenal and spleen indices occurred in the winter, indicating these months as the period of greatest stress. Significant negative correlations of the adrenal index and mean temperature of adult rats indicate that adrenal hypertrophy was due to cold stress. Similarly, the composite (all age classes and sex combined) sample showed significant negative correlations of the spleen index and freeze free days.

Lower adrenal and spleen indices occurred in the spring

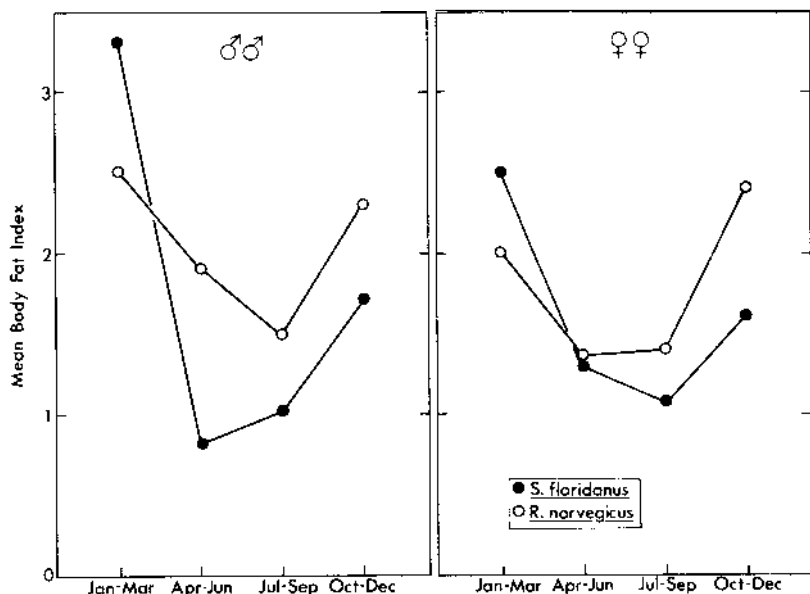


Fig. 18. Comparison of Seasonal Fluctuations in Mean Body Fat Indices of Norway Rats and Eastern Cottontail Rabbits (Bittner and Chapman in press) Collected on St. Clements Island (1976-1978).

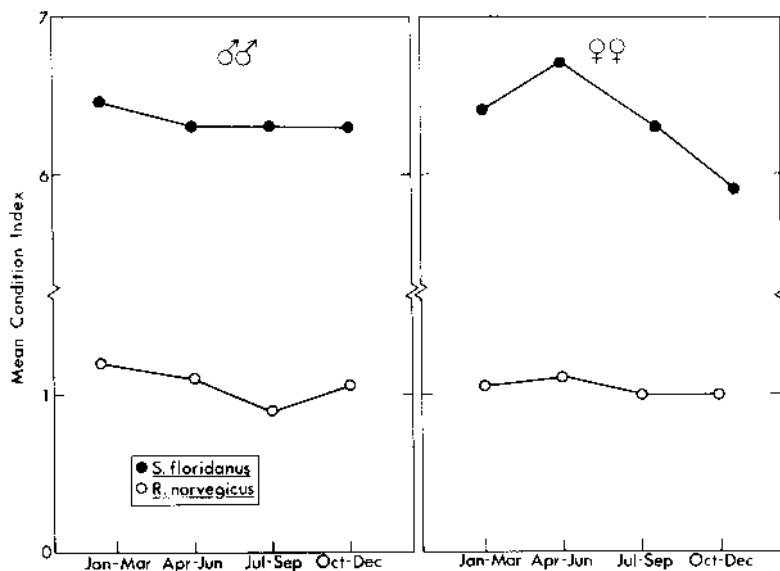


Fig. 19. Comparison of Seasonal Fluctuations in Mean Condition Indices of Norway Rats and Eastern Cottontail Rabbits (Bittner and Chapman in press) Collected on St. Clements Island (1976-1978).

Lower adrenal and spleen indices occurred in the spring and summer when reproductive activity was greatest and density was highest. This relationship suggests that reproductive activity and higher densities was not stressful to the rats on St. Clements Island.

The results of this study indicate that the rat population on St. Clements Island is similar to rural rat populations in reproductive parameters and response to seasonal climatic variation. Reproductive parameters of the St. Clements Island population is found to be generally lower than those of urban rat populations. This difference can be attributed, in part, to population density control mechanisms. High density urban rats tend to have higher reproductive rates, greater intrauterine mortality and greater stress at high densities, regardless of season. Rural rats and the St. Clements population on the other hand are characterized by lower reproductive rates, a distinct breeding season, lower intrauterine mortality and greater stress during the winter, regardless of density.

#### SUMMARY

1. The reproductive and physiological responses of the Norway rat were studied on St. Clements Island, southern Maryland, from August 1976 to February 1978.
2. Four condition indices were used to assess the responses of Norway rats to environmental stress: (1) the condition index (K), (2) the adrenal index (AI), (3) the spleen index (SI), and (4) the body fat index (BFI).
3. The mean population estimate for the sample period November 1976 to March 1977 was  $26 \pm 4$  rats. Estimated mean population size for the sample periods April to June 1977 and June to October 1977 was  $37 \pm 18$  rats and 60 22 rats, respectively. Rat population on St. Clements Island increased approximately 44 percent from the winter of 1976-77 to the winter of 1977-78.
4. The maximum density of rats on St. Clements Island was estimated to be 3.30 rats per hectare.
5. The overall sex ratio of Norway rats collected on St. Clements Island was 84.5 males per 100 females. The

fetal sex ratio was 113 males per 100 females. Neither was significantly different from a 1:1 ratio.

6. The duration of the breeding season for female rats was approximately 237 days per year. Males were reproductively active throughout the year. Peak reproductive activity of females occurred in June and July.
7. The mean litter size of Norway rats with viable fetuses was 8.83. Seasonal variation was not significant.
8. The mean ovulation rate based on corpora lutea counts of pregnant female rats was 10.39. More implantations occurred in the right uterine horn than the left.
9. Analysis of the relationship between the mean ovulation rate and mean litter size indicated that 15 percent of the ovulated eggs failed to implant or were resorbed.
10. The estimated productivity of rats on St. Clements Island was 23.5 young per adult female per year.
11. The condition index was relatively stable throughout the year for both sexes. Adults had significantly higher condition indices than juveniles.
12. A highly significant difference in the adrenal index was found between the sexes. Males had consistently lower adrenal indices than females throughout the year. Combined adrenal weights showed the left gland to be significantly heavier than the right.
13. Peaks in the adrenal indices of female rats occurred in the winter. Adult rats showed negative correlations of the adrenal index and mean temperature. Juveniles showed positive correlations of the adrenal index with freeze free days.
14. The mean spleen index was significantly different for sex and age. Females had a higher spleen index than males, and adults had higher indices than juveniles. Adults and subadults had significantly higher spleen indices in the winter.
15. The body fat index was similar for the sexes and all age classes. Differences in the body fat index showed a significant drop from winter to summer and a significant increase from summer to fall.
16. A highly significant negative correlation was found between the adrenal index and condition index for the composite sample. Adults showed significant negative

correlations between the spleen index and body fat index. Juveniles showed significant positive correlations of the spleen index and the condition index.

17. Differences observed between the St. Clements Island rats and previously reported data on rural and urban rat populations suggest different mechanisms, influencing population parameters—one in which high urban population densities inhibit reproductive function causing population declines irrespective of season, and another in which climatic extremes reduce low density rural populations at seasonal intervals.
18. The study indicated that the St. Clements Island population was similar to rural rat populations in reproductive parameters and response to seasonal climatic variation. When compared to urban populations, the St. Clements Island population and rural populations were found to have lower reproductive rates, a distinct breeding season, lower intrauterine mortality and greater stress during the winter, regardless of the density.
19. The simultaneous study of the eastern cottontail population on St. Clements Island (Bittner and Chapman in press) allowed comparison of rodents and lagomorphs to identical climatic and habitat conditions under a confined situation. Distinct differences were observed in the physiological responses of the two orders.

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